BODY SIZE RELATIONSHIPS AND REPRODUCTIVE ECOLOGY OF FEMALE FERAL HORSES ON SABLE ISLAND, NOVA SCOTIA

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By

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ABSTRACT

Body size is an important determinant of reproduction in capital breeding animals, including large mammals. However, it is not always practical to hand-measure body size of free-ranging species. In recent years, parallel-laser photogrammetry has been used to obtain remote estimates of body size for some animals, though it remains unknown how well this technique might capture variation in curvilinear body features or if the distance between parallel-laser calipers is altered when projected onto a curved surface. In this thesis, I describe a photogrammetric system that may be useful for obtaining body-size measurements from unrestrained large mammals that permit approach, using domestic horses (*Equus ferus caballus*) as a model (Chapter 2). I then apply this technique in the field to a wild (feral) population of horses at Sable Island National Park Reserve, Nova Scotia, Canada, where I include body size measurements as variables in a detailed analysis of factors affecting reproduction in females (Chapter 3). Using my parallel-laser photogrammetric system, I show how curvilinear hand-measurements (e.g., across the barrel of a horse) are stongly correlated with their respective linear photogrammetric estimates ($R^2 \geq 0.998$), and most photogrammetric estimates using my system had high reliability. Using three variables of body size, photogrammetric estimates and hand-measurements explained 86.0% and 96.2%, respectively, of the variation in body weight of a sample of domestic Newfoundland ponies. On Sable Island, Nova Scotia, I examined the relationship of numerous variables (including skeletal body size and body condition) with the probability of yearly reproductive success for female Sable Island horses (years 2008–2012), where I define reproductive success as production of an offspring surviving to one year of age. Age class was a dominant factor predicting reproductive success, as expected from trends previously associated with body size or reproductive experience

in other populations. Age-class specific energy budgets or social and sexual behaviour caused a more pronounced relationship with body condition at parturition in sub-adults, and body condition at conception and stability of consort relationships were associated with reproductive success in adults. In addition, relationships with local density suggested limited forage around the time of conception and limited water during lactation might also influence reproductive success in adult females. Although relationships were evident for age class, which is correlated with body size, reproductive success was not related to skeletal body size, past reproductive experience, age of primiparity, or band structure. The capital breeding strategy and year-round social associations seen in horses make their reproductive ecology a combination of patterns observed for large ungulates and social primates.

PREFACE

My thesis has five chapters. Chapter 1 is a general introduction and a description of overall research goals. Chapter 2 is a verification of my parallel-laser photogrammetric technique and I identified variables that explain variation in body size of horses. Chapter 3 is a study of the reproductive ecology of female horses on Sable Island. Chapter 4 is my general conclusions and suggestions for future research. Chapter 5 is a list of literature cited. The results presented in Chapter 2 have been accepted for publication in the *Wildlife Society Bulletin*:

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LIST OF ABBREVIATIONS AND NOTATIONS

ANOVA: Analysis of variance

CI: Confidence interval

GLMM: Generalized linear mixed effects model

ICC: Intraclass correlation coefficient

ID: Identity

NAO: North Atlantic Oscillation

SLP: Sea level pressure

YRS: Yearly reproductive success

1.0 GENERAL INTRODUCTION

Population dynamics of large ungulates with high adult survival rates are expected to be determined principally by female reproductive rates and juvenile survival (Gaillard et al. 2000b), making the study of female reproductive ecology important for the management and conservation of large mammals (Sibly et al. 2005). The reproductive ecology of female ungulates can be very complex. Reproductive rates of young females are often low and can be highly variable, whereas those of prime-age females are typically high and show little variation over time (Gaillard et al. 2000b). Within a population, individual reproductive output may be affected by density (Gaillard et al. 2000b), age (Festa-Bianchet 1988), environment (Berger 1986), weather (Welsh 1975), life history (e.g., reproductive experience, Cameron et al. 2000), socio-ecology (e.g., social integration, Cameron et al. 2009) and body size or mass (Albon et al. 1983). Of these variables, body size information is one of the most difficult to acquire, particularly when data for a large sample are required.

Measurement of recently-deceased individuals is commonly used to obtain body size or mass data, particularly for large mammals (e.g., larder weights of red deer, Albon et al. 1983; moose, Sand 1996, caribou, Couturier et al. 2010); however, this precludes repeated measurements during an individual's lifetime to obtain variables of growth rate. For the latter, capture and handling of live animals with release of subjects following measurement is required. While smaller ungulates may be handled with relative ease (e.g., roe deer, Gaillard et al. 1997; Soay sheep, Pelletier et al. 2007), larger species may require immobilization to allow handling (feral horses, Berger et al. 1983; mountain goats, Côté et al. 1998). Confining stalls or other physical immobilization devices may be used to obtain body size estimates of some large

animals without chemical immobilization (bison, Green and Rothstein 1991); however, measurements that can be performed safely are often restricted. Capturing, chemically immobilizing and handling animals can also be expensive, and is potentially harmful to subjects (e.g., mortality due to human error, Berger et al. 1983) or may temporarily reduce their fitness (e.g., reduced fighting ability; Pelletier et al. 2004; decreased offspring production, increased offspring abandonment, Côté et al. 1998). If the study of reproductive ecology is the goal of the study, data collection techniques that are invasive and have the potential to affect reproductive rates and offspring survival are not ideal.

Non-invasive, remote estimation of body size for the purpose of studying growth rates and effects on life history traits using the techniques of photogrammetry is becoming more common in ecological studies (e.g., Bergeron et al. 2010). Photogrammetry is the measurement of objects in photographs or digital images (Deakos 2010; Berger 2012). Photogrammetry can be used to provide measurements of large numbers of free-ranging animals and is relatively inexpensive (Berger 2012). Some photogrammetric techniques can produce accurate measurements of animals several hundred meters from observers (Willisch et al. 2013), although most methods are only accurate when used at distances less than 20 m (Berger 2012). Its application as a tool to measure body size is thus well suited for species that are approachable though perhaps difficult to handle, or where concern exists about the potential for handling to have negative effects on the reproductive rates of subjects or the survival of their offspring.

One species that may fit the description of an animal that would be difficult to study questions related to morphology with direct handling, but may in some circumstances be highly approachable is the feral horse. Where feral horses are not subject to direct human handling, shooting, or other interference, and where there are no predators, they can be quite approachable.

An example of this occurs on Sable Island, Nova Scotia, Canada. The island is home to several hundred feral horses (N = 552 in August, 2014) that have ranged freely for well over two centuries (Christie 1995; Plante et al. 2007). The population has been genetically isolated since at least 1935 when the last recorded introduction of breeding stock occured (Welsh 1975) and in 1960 the horses became legally protected from human interference through the Sable Island Regulations of the Canada Shipping Act (de Villiers and Hirtle 2006). In December, 2013, Sable Island became a National Park Reserve, and is now protected under the Canada National Parks Act.

The feral horses of Sable Island live in a natural though simplified environment without predation, human interference, or interspecific competition (they are the island's only terrestrial mammal and are unmanaged). The population is subject to an individual-based monitoring program by the University of Saskatchewan with respect to movements, behaviour, group membership, and life history, where all members of the population are identified and followed (801 life histories from 2008–2013, N = 14,347 locations; see Contasti et al. 2012, 2013; Marjamäki et al. 2013; van Beest et al. 2014). Data are collected annually during the late breeding season (summer) using a standardized, weekly walking census. Sable Island offers a unique situation for studying ecological processes related to population dynamics: it is a closed system that lacks trees allowing field observers to easily spot the majority of animals in an area; there are no predators; and no other guild members are present to compete with horses for forage. In addition to the auspicious conditions on Sable Island, there are several interesting aspects about horses with respect to studying reproductive ecology compared to other large mammals: they are monotocous (i.e., a fixed litter size of one, Gaillard et al. 2000b), simplifying the criteria for successful reproduction compared to polytocous animals (i.e., variable litter size,

Gaillard et al. 2000b); individuals can be identified using unique features and coat patterns, so handling animals is unnecessary; and horses have a unique social system more akin to that of primates.

Feral horses exhibit female-defense polygyny (Linklater 2000). This mating system is a result of their social organization. Unlike many polygynous mammals, where males and females only associate during mating periods, horses and several other equid species establish relatively stable, long-term relationships with consorts that can last several years (Clutton-Brock 1989; Linklater 2000; Feh 2005). These long-term, consort relationships result in non-territorial groups called family bands that are composed of a dominant stallion, one or more mares, their pre-dispersal offspring and sometimes one or more tag stallions (i.e., subordinate adult males, Rubenstein 1981). Dominant band stallions perform the majority of copulations, defending their harem from bachelors and subordinate stallions (Feh 2005; Contasti 2011). Family bands are the main reproductive unit in the female-defense polygyny mating system exhibited by horses (Linklater et al. 1999), but other social associations also exist.

Apart from family bands, feral horses may found be in mixed sub-adult groups, unstable bachelor groups or as solitary individuals (Linklater 2000; Contasti 2011). Bachelor groups are composed of both young males that have recently dispersed from their natal band and adult bachelors. Mixed sub-adult groups are composed of young females and males, none of which have offspring, and these groups are typically unstable (Contasti 2011). Solitary individuals are usually young males dispersing from natal bands or bachelors (Contasti 2011). Although mixed-sex associations of sub-adults are rare in feral horse populations, the other social associations are commonly found (Berger 1986; Linklater 2000; Contasti 2011).

Although family bands are stable, intergroup movement—voluntary or not—occurs throughout the year on Sable Island. Band membership changes most commonly result from natal dispersal—usually when offspring are one to three years old—however mares also moved between family bands (Contasti 2011). Young males often dispersed to bachelor groups and young females to other family bands (Contasti 2011). Intergroup movements of mares typically occurred between parturition periods, and natal dispersal between fall and early summer (Contasti 2011). Bachelor stallions challenged band stallions or formed new family bands most frequently between fall and early summer (Contasti 2011).

1.1 Research Objectives

Density, age class, weather, socio-ecology, life history, body size and body condition can affect individual reproductive output in large mammals. Individual-specific information for all but one of these factors—body size—has been obtained for Sable Island horses with tested, non-invasive techniques. In order to use body size to address questions about ecology and evolution, I needed to evaluate a non-invasive technique to obtain body size measures. Here I evaluate the accuracy of photogrammetry to remotely estimate body size of feral horses. Testing such a system was my primary research objective for Chapter 2, where I aimed to:

1) Select a photogrammetry technique to remotely estimate body size in free-ranging mammals;

2) Validate the technique using a sample of domestic horses of similar conformation and size to that of the Sable Island horses (I used Newfoundland ponies as a surrogate) and determine its accuracy; and,

3) Identify important body size variables that can be used for feral horses.

After I had tested my photogrammetric technique and identified body size variables for use on feral horses, I applied the technique to the feral horse population on Sable Island and use body size information to investigate the reproductive ecology of females. My objectives for Chapter 3 were to:

1) Examine the effect of local density, winter weather, social factors, reproductive experience and body size and condition on the probability of yearly reproductive success of female horses; and,

2) Examine the effect of early reproductive effort on subsequent reproductive success in feral horses.

Studies of female reproductive ecology use many different variables to measure fitness and choice of fitness variables can limit the implications of research. By defining reproductive success as the production of an offspring that survives to weaning (i.e., one year of age), I incorporated both reproductive rates and early juvenile survival into one variable. Since the majority of juvenile mortality occurs within one year of birth (Welsh 1975; Berger 1986), foals

that survive to weaning are more likely to contribute to population growth (Welsh 1975). Therefore, my research will provide more direct insights about the contribution that different ecological factors have on the population dynamics of Sable Island horses.

2.0 PARALLEL-LASER PHOTOGRAMMETRY TO ESTIMATE BODY SIZE IN FREE-RANGING MAMMALS

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2.1 Introduction

Body size is an important determinant of reproduction (Green and Rothstein 1991) and survival (Gaillard et al. 2000a), affecting fitness through both natural (Coltman et al. 1999) and sexual selection (McElligott et al. 2001; Preston et al. 2003). Within a species, body size can be influenced by several ecological factors including climate (Post et al. 1997), resource availability (Yom-Tov et al. 2010), and competition (e.g., conspecific density, Pettorelli et al. 2002). More recently, metrics of body size collected through long-term studies of mammals have led to insights into eco-evolutionary dynamics, such as how variation in body size might interact with environmental factors to affect population dynamics in Soay sheep (*Ovis aries*, Pelletier et al. 2007). By measuring body sizes of live animals, Pelletier et al. (2007) were able to incorporate effects of size at different developmental stages over time and factor in an individual's contribution to population growth based on its morphometrics for a given year. Repeatedly measuring body size in long-term ecological studies is advantageous because it allows body size

at different developmental stages and in different years to be analyzed in relation to individual life history.

Hand-measuring body size of live animals is not always easy. Handling may be stressful for the subject or expensive if immobilization is required. It also may be impractical for large animals that are often difficult to handle, even if a researcher can approach targets relatively closely (e.g., seals [Phocidae], whales [Cetacea], some herbivores including those habituated to humans). Sable Island, Nova Scotia, Canada is home to a population of several hundred feral horses (*Equus ferus caballus*). In 2007, the University of Saskatchewan initiated an intense, individual-based monitoring program to answer key questions in ecology and evolution (e.g., van Beest et al. 2014), including those related to body size. These horses are wild (feral) yet approachable (to within 5 m), allowing unhindered observation and sample collection; however, their large size—and my intention to study this population using minimally invasive methods—made capture, immobilization, or handling an impossibility for obtaining body size measurements. Remotely measuring body size using digital photogrammetry presented itself as a promising solution for my needs.

The main difficulty to successful photogrammetry is correctly and consistently establishing scale in photographs so that objects may be accurately measured. There are several techniques available to establish scale for single-camera photogrammetry such as using the ratio of distance from the subject to camera and lens focal length (e.g., Breuer et al. 2007), or placing an object of known size near the subject (e.g., Thompson 1995). An increasingly common method uses two parallel lasers projected on the subject to introduce scale (e.g., Durban and Parsons 2006; Bergeron 2007; Rothman et al. 2008; Webster et al. 2010). Parallel-laser beams are equidistant apart regardless of distance from their apertures (Bergeron 2007). For scale to be

introduced correctly to a photograph, the lasers and camera must be orthogonal to the surface of the animal (Durban and Parsons 2006; Deakos 2010); therefore, lasers are typically mounted to a camera so that a researcher must only position the unit perpendicular to the object to be measured.

Laser photogrammetry has been used to estimate measurements of relatively flat body surfaces in several aquatic and terrestrial vertebrates (e.g., *Capra ibex*, Bergeron 2007; *Procolobus rufomitratus*, Rothman et al. 2008; *Manta alfredi*, Deakos 2010; *Cephalorhynchus hectori*, Webster et al. 2010). These studies rely on linear photogrammetric estimates of desired linear morphometrics or traits; however, body size of most large mammals (including horses) may be best represented with measurements of curved body surfaces (e.g., Carroll and Huntington 1988). Photographs are two-dimensional, photogrammetry represents curvilinear features with linear estimates (see Fig. 2.1). It is not known how well these linear photogrammetric estimates may be correlated with curvilinear hand-measurements (Bergeron 2007), or how well these estimates represent general conformation or body weight of animals.

Here I describe a system of parallel-laser photogrammetry for obtaining remote estimates of body size. My specific objectives included: 1) examining whether projecting lasers onto a curved surface corrupted their scale; 2) examining whether parallel-laser photogrammetry can accurately and reliably measure curvilinear features of large mammals; 3) identifying variables of body size that represent variation in body weight; and 4) comparing the ability of photogrammetric and hand-measurement techniques to explain variation in body weight.

2.2 Materials and Methods

2.2.1 Laser photogrammetry equipment

To measure horses, I modified the device used and described by Bergeron (2007) and Rothman et al. (2008). The parallel-laser caliper apparatus (hereafter, laser standard; Fig. 2.2) has a rectangular aluminum frame with gun rail mounts projecting laterally. I mounted a pair of green laser-sights (AimSHOT, Alpharetta, GA) on the gun-rail mounts with their beams projecting parallel 19.05 cm apart. I used class IIIa, 5 mW, 532-nm green lasers because they are more visible in bright daylight than are red lasers and are unlikely to cause damage to the subject's eye if brief, accidental exposure occurred. Windage- and elevation-set screws in the laser-sight casings facilitated adjustment of the lasers in the field to ensure they were parallel. I mounted a Nikon CoolPix L810 digital camera (Nikon Imaging Inc., Tokyo, Japan) with a 0.635 cm (1/4") bolt 1 cm above the top of the laser housings allowing the camera's lens to be centered between them; laser beams projected around the center of photographs when parallel as a result. The bottom plate of the aluminum frame had 0.635-cm and 0.953-cm (3/8") threaded bores to attach a monopod or tripod for stability.

2.2.2 Calibration

I used a flat target with a 19.05-cm × 19.05-cm black square printed on it, referred to as the DigiTarget™ (Digicontractor Inc., Tarzana, CA) to ensure the lasers were parallel in the field. I projected the lasers onto the DigiTarget™ and adjusted the set screws so that the center of each

laser beam aligned with the outer edges. I ensured the laser standard was calibrated at 5 m and 10 m from the DigiTarget™ before using the laser standard. I confirmed that the laser standard remained parallel and set to the correct distance after each use.

2.2.3 Data collection

I collected all morphometric data from domestic Newfoundland ponies at the Newfmist Newfoundland Ponies farm near Radisson, Saskatchewan, Canada. I conducted the sampling according to the University of Saskatchewan Animal Care Protocol 20090032.

I sampled 30 individuals (5 ad uncastrated male, 9 ad castrated male, 16 ad female) of known age (i.e., 4 to 22 years); none of the mares were pregnant. I weighed each pony to the nearest 0.5 kg, with a portable livestock scale immediately preceding measurement (Table 2.1). I positioned ponies so that their forelimbs were straight and head erect. I hand-measured the subjects for body length, sternum-pin length, withers-pin length, barrel length, croup length, withers-knee length, barrel depth, heart depth, withers-chest depth, forequarters depth, forelimb cannon length, tibia length and hindlimb cannon length with a flexible measuring tape to the nearest 0.5 cm (Tables 2.1 and 2.2; Fig. 2.3).

Standing between 5 m and 10 m from the subject, I took several photos of each pony in the same posture as before with the laser standard projected horizontally onto its barrel and the camera zoomed completely out. I visually assessed photos for quality. There were a limited number of appropriate photographs for some individuals and I desired an equal number of replicates among the horses; hence, I only measured photographs where ponies had appropriate posture and appeared orthogonal to the lasers. I measured two photographs from each subject

using the photogrammetric software iPhotoMEASURE Standard Edition Version 2.1 (Digicontractor Inc., Tarzana, CA, USA) and calculated average photogrammetric estimates of each morphometric for every individual in centimeters (Table 2.1). I measured photogrammetric estimates from the same landmarks as hand-measurements.

Equids carry much of their body fat subcutaneously rather than around internal organs (e.g., kidneys), as is common in other ungulates (Huntington and Cleland 1992). Thus, body condition scores correlate strongly with body fat and live weight in equids (Henneke et al. 1983). I scored body condition as outlined by Carroll and Huntington (1988) from photographs obtained while measuring subjects. This index ranges from 0 (very poor condition) to 5 (obese), with half-point gradations when different regions of the body varied in score.

2.2.4 Statistical analyses

To validate my parallel-laser technique, I used linear regressions forced through the origin to compare each photogrammetric estimate with its analogous hand-measurement (Bergeron 2007; Rothman et al. 2008). I forced these models through the origin because as the distance between two landmarks approaches 0 cm, hand-measurements and photogrammetric estimates must both approach 0 cm until both landmarks are at the same location. For linear morphometrics, a regression slope of 1 indicates that photogrammetric estimates are unbiased because photogrammetric estimates and hand-measurements quantify the same distance (Bergeron 2007). However, when morphometrics are curvilinear, linear photogrammetric estimates will be shorter than their analogous hand-measurement (see Fig. 2.1) and regression slopes will be >1 when the hand-measurement is on the y-axis.

I assessed the reliability of the nonaveraged, photogrammetric estimates for each measurement with intra-class correlation coefficients. I estimated intra-class correlation coefficients and 95% confidence intervals using the variance components from a 1-way analysis of variance (ANOVA). I also calculated the intra- and inter-individual variation in my photogrammetric estimates for each morphometric.

Body condition can be a strong predictor of variation in weight (Carroll and Huntington 1988). I used a 1-way ANOVA to determine if any relationship existed. I aimed to identify important variables of body size that represented variation in weight using multiple regression. High collinearity between covariates in a multiple regression can confound the identification of relationships between covariates and the response variable (Mason and Perreault 1991; Zuur et al. 2010). Hence, I evaluated multicollinearity among morphometric variables using Pearson's correlation coefficient (r). When covariates were highly correlated (i.e., $r > 0.7$), I included only one variable to represent that aspect of body size. Because I was later applying this technique to feral horses, I preferred morphometric variables that not only would allow comparison with other studies but also are commonly visible in field photographs (e.g., distal limbs are often obscured by tall vegetation, and might not be measured easily in the field). I included heart depth, sternum-pin length, withers-knee length, forelimb cannon length and tibia length in my multiple regression analysis.

I constructed a global model that modeled weight with these hand-measurements and performed stepwise, backward-elimination model selection (Mac Nally 2000; Burnham and Anderson 2002). I used Akaike's Information Criterion corrected for small sample size (AIC_c, Burnham and Anderson 2002) to identify variables for deletion. I removed variables until ΔAIC_c relative to the lowest AIC_c was >2.0 (Burnham and Anderson 2002). Out of this final set, I

selected the model with the smallest AIC_c (Burnham and Anderson 2002). I used Akaike weights to indicate the probability that a particular model is the best Kullback-Leibler model (Burnham and Anderson 2002). I modeled variation in body weight with the analogous set of photogrammetric estimates included in the selected model. I used ΔAIC_c to compare the ability of the two measurement techniques to explain variation in body weight.

I tested for homogeneity of variance among groups for data analyzed with ANOVA (Zuur et al. 2010). I confirmed the residuals of all regressions for normality with QQ-plots (Zuur et al. 2010). I checked for influential observations using the Cook statistic (Zuur et al. 2010). All statistical analyses were performed with R Version 3.0.2 (R Core Team 2013).

2.3 Results

Photogrammetric estimates were strongly correlated with hand-measurements for all morphometrics (all $R^2 \geq 0.998$, Table 2.3). Regression slopes of linear features (i.e., fore- and hindlimb cannon length) were ~1, indicating that photogrammetric estimates were unbiased compared to linear hand-measurements. Slopes of regression for curvilinear features were >1, indicating that linear photogrammetric estimates underestimated curvilinear hand-measurements as expected. I identified four observations that had higher leverage and were potentially influential for the linear regression comparing tibia length. Inclusion of these observations in the model had minor influence on the slope, but the standard error increased by approximately 155% compared to when they were omitted (Table 2.3).

Most photogrammetric estimates had high intra-class correlation coefficients (i.e., > 0.8; Table 2.1). Photogrammetric estimates of barrel length, forequarters depth, tibia length, forelimb

cannon length and hindlimb cannon length had lower intra-class correlation coefficients (i.e., approximately 0.7 or less). Forequarters depth, barrel length, and withers-pin length had the highest intra-individual variation between photogrammetric estimates (Table 2.1).

There was little variation in body condition ($\bar{x}$ = 3.02, SD = 0.28). As a result, weight was not significantly related with body condition score (ANOVA, $F_{2,27}$ = 2.543, P = 0.097). Weight was best predicted by hand-measurements of heart depth, sternum-pin length, and withers-knee length (Table 2.4). Specifically, weight = 4.90 [0.91SE] × heart depth + 2.87 [0.49] × sternum-pin length + 2.52 [0.94] × withers-knee length − 683.38 [45.59] (R^2 = 0.962). When the same model was fit with the analogous photogrammetric estimates (weight = 6.14 [3.27SE] × heart depth + 6.55 [1.18] × sternum-pin length + 0.335 [2.10] × withers-knee length − 697.16 [104.21]; R^2 = 0.860), it explained less variation in weight than the model for hand-measurements (ΔAIC_c = 39.46).

2.4 Discussion

I show that linear photogrammetric estimates may be used to obtain accurate approximations of body size in a large herbivore. Based on the regression slopes for linear morphometrics, the laser photogrammetric system had comparable accuracy to those used by Bergeron (2007) and Rothman et al. (2008). This holds as long as the beams are projected perpendicular to the plane measured in a photograph and are a similar distance from the camera. Although laser beams are projected onto a curved surface, the linear distance between them remains unchanged because photographs are two-dimensional. It is the curvilinear distance of the surface between the beams (which is neither presented by nor measured in the photograph) that would deviate. Hence,

projecting lasers perpendicularly onto a slightly curved surface will not significantly alter the distance between the beams and scale can be established correctly in a photograph.

In my study, photogrammetric estimates underestimated their respective hand-measurements for curvilinear morphometrics. On account of this inherent underestimation, regression slopes cannot be used to indicate accuracy. However, I found that inter-method comparisons for curvilinear morphometrics have high correlations, suggesting that the photogrammetric estimates strongly reflect hand-measurements.

I found most photogrammetric estimates have "substantial" reliability (i.e., intra-class correlation coefficients > 0.8, Shrout 1998). Given that averaging replicate measurements usually improves reliability (Shrout 1998), my averaged photogrammetric estimates likely detected variation between individuals for morphometrics with substantial reliability. Intra-class correlation coefficients are affected by intra-subject variation in relation to inter-subject variation (Shrout 1998; Weir 2005). Although forelimb cannon length and hindlimb cannon length had smaller intra-individual variation than some of my more reliable measurements, their low inter-individual variation resulted in only fair to moderate reliability (i.e., intra-class correlation coefficients >0.40 but <0.80, Shrout 1998). Therefore, these measurements might be precise, but they are not useful to adequately detect inter-individual variation.

Skeletal landmarks that are moveable or difficult to identify in photos may result in measurement error. The highest, most posterior spinous process at the withers may be ambiguous and the point of the shoulder is very mobile and only evident by contrast and texture on the coat for horses having high body condition (subcutaneous fat reserves). The landmarks for tibia length were also difficult to identify, depending on how the hind leg is positioned. Inconsistency when identifying landmarks caused random measurement error (Weir 2005), leading to high

intra-individual variation for tibia length and several measurements that have withers or point of the shoulder as landmarks (i.e., forequarters depth, barrel length, and withers-pin length**)**. Inconsistent identification of skeletal landmarks due to posture in combination with low inter-individual variation is the likely cause of the influential points identified for tibia length during model checking. Consequently, measurements prone to measurement error should be avoided, particularly when inter-individual variation is low.

Similar to Carroll and Huntington (1988), I found that heart depth, a measurement of body length, and height were important variables when explaining variation in weight with hand-measurements. I did not find weight was significantly affected by body condition, suggesting the majority of variation in weight was due to variation in skeletal size (Carroll and Huntington 1988).

All of the measurements I used to estimate body weight were curvilinear morphometrics. The inability of photogrammetric estimates to measure variation in the depth of curvilinear traits that is represented in hand-measurements is the reason hand-measurements explained variation in body weight better. Despite having lower explanatory power, photogrammetric estimates did explain a large proportion of variation in weight, suggesting that estimates of curvilinear morphometrics can capture variation in size and their usefulness in ecological studies should not be discounted.

The technique I describe is an inexpensive means by which to acquire body size information for large numbers of individuals, particularly those that may be approached relatively closely or are habituated to humans. Blinds or vehicles may allow the technique to be used around bait or common feeding, watering, and resting sites for less approachable species (Bergeron 2007). Unlike other measurement methods that require teams to capture and handle

animals, the laser standard system I describe can be operated by one person. For example, with a single researcher collecting photographs, I was able to obtain data for approximately 90% of the Sable Island horse population in 2012 (>400 horses).

I found that lasers rarely became misaligned in the field; however, this may occur, and lasers should be verified for proper alignment at several points throughout a sampling. It is important to only take photographs of animals when they are within the range that calibration of the lasers encompassed (e.g., I calibrated my lasers for horses located between 5 m and 10 m from the camera).

Although I provide a proof of principle, some of the results provided here are only applicable for mammals with similar morphometrics to horses (i.e., wild equids, such as Przewalski's horse [*Equus przewalskii*], zebra [*Equus* spp.] and ass [*Equus* spp.]). Small pilot studies identifying ideal measurements for other species and their relationships with weight (or other variables of interest) should be performed prior to application of the technique on target populations.

Figure 2.1. Adult female Sable Island horse, August, 2013. The curvilinear hand-measurement of barrel depth (a) is longer than the linear photogrammetric estimate (b). Photo by J. Weisgerber.

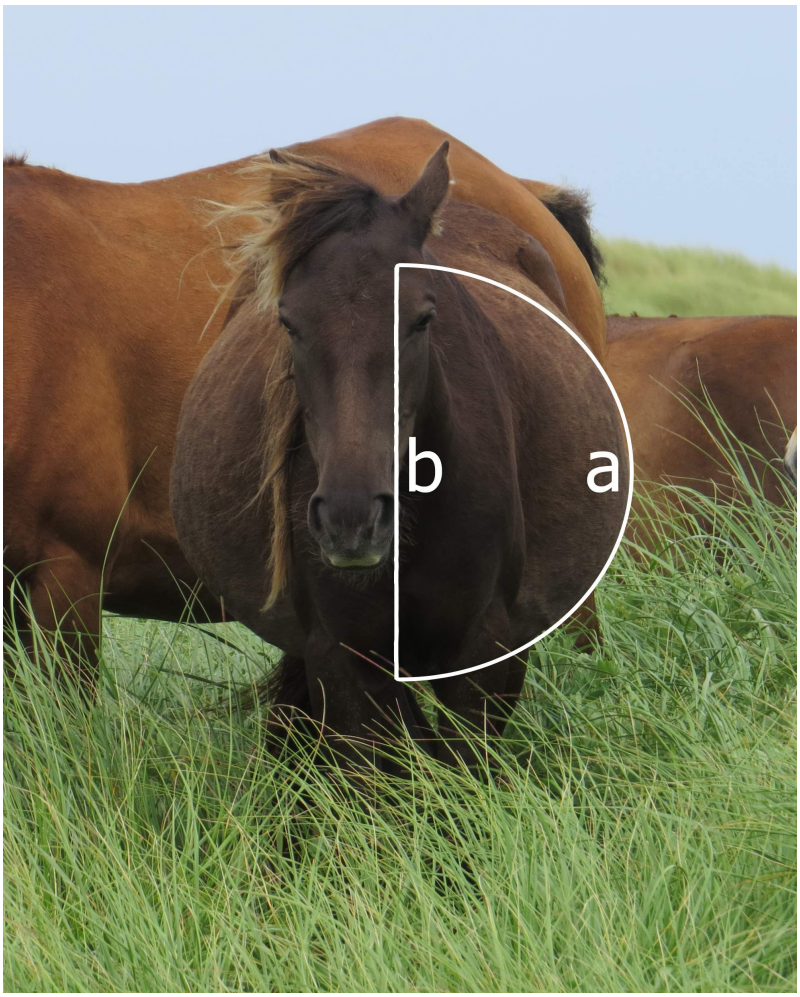

Figure 2.2. Parallel-laser standard apparatus used to photograph domestic Newfoundland ponies near Radisson, Saskatchewan, Canada in October, 2013, for photogrammetric analysis. The components are LEFT: (a) camera, (b) laser sights, (c) aluminum frame, (d) 1/4” (0.635-cm, front) and 3/8” (0.953-cm, back) threaded bores to attach mono-/tripod, (e) gun rail mounts, RIGHT: (f) windage–elevation adjustment set screws and (g) twist on/off power switch. Photo by J. Weisgerber.

Figure 2.3. Morphometrics measured on domestic Newfoundland ponies near Radisson, Saskatchewan, Canada, by hand with a flexible measuring tape and from photos in October, 2013. The two green laser dots visible on the barrel (L and R) are projected from the laser standard. They are 19.05 cm apart and are used to establish scale in the photograph. The measurements are (1) body length, (2) withers-pin length, (3) sternum-pin length, (4) withers-knee length, (5) barrel length, (6) croup length, (7) barrel depth, (8) heart depth, (9) withers-chest depth, (10) forequarters depth, (11) tibia length, (12) forelimb cannon length, (13) hindlimb cannon length. Numbers refer to nearest line. Photo by J. Weisgerber.

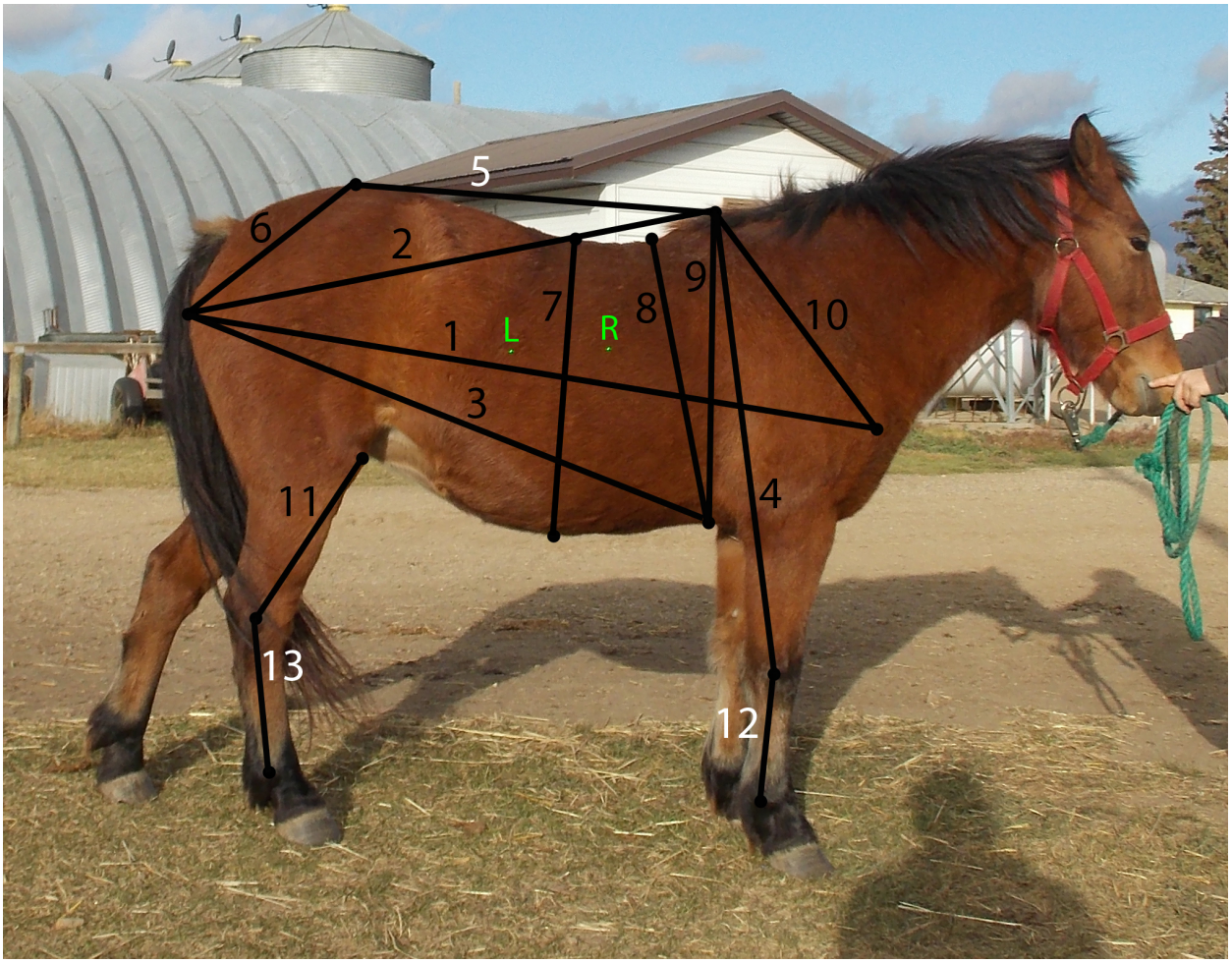

Table 2.1. Summary of body size and weight data collected from domestic Newfoundland ponies near Radisson, Saskatchewan, Canada, in October, 2013 (n = 30). Body weight is measured in kilograms with a portable livestock scale. Intra-class correlation coefficients (ICC) and their 95% upper and lower confidence intervals (upper and lower CI, respectively) are unitless. Intra- and inter-individual variation (intra and inter, respectively) and all other measurements are recorded in centimeters. Hand-measurements were performed with a flexible measuring tape and photogrammetric estimates were performed using the photogrammetric software iPhotoMEASURE (Digicontractor, Inc., Tarzana, CA).

	Hand-measurements		Photogrammetric estimates						
Morphometric	$\bar{x}$	**SE**	$\bar{x}$	**SE**	**ICC**	**Upper CI**	**Lower CI**	**Intra**	**Inter**
Body length	144.0	1.6	126.8	1.2	0.959	0.980	0.916	1.89	43.75
Withers-pin length	119.4	1.2	100.7	1.0	0.891	0.946	0.786	3.73	30.54
Sternum-pin length	125.6	1.4	99.7	1.1	0.978	0.989	0.954	0.75	32.45
Withers-knee length	99.7	0.9	87.3	0.6	0.834	0.917	0.683	2.20	11.06
Barrel length	77.0	0.8	68.2	0.7	0.712	0.851	0.481	4.76	11.77
Croup length	44.2	0.6	39.5	0.5	0.869	0.932	0.734	1.14	7.21
Barrel depth	94.2	1.3	56.2	0.6	0.977	0.989	0.952	0.28	11.57
Heart depth	80.5	0.9	55.1	0.4	0.945	0.973	0.889	0.32	5.49
Withers-chest depth	79.5	0.9	59.8	0.5	0.892	0.947	0.787	0.72	5.95
Forequarters depth	56.3	0.6	48.7	0.5	0.655	0.819	0.395	2.57	4.87
Tibia length	41.9	0.4	36.7	0.4	0.708	0.856	0.434	1.60	3.89
Forelimb cannon length	22.8	0.3	22.7	0.2	0.578	0.773	0.285	0.71	0.97
Hindlimb cannon length	32.1	0.3	30.3	0.3	0.622	0.809	0.295	0.81	1.34
Body weight	323.3	10.0							

Table 2.2. Morphometrics measured on domestic Newfoundland ponies near Radisson, Saskatchewan, Canada, in October 2013, and a description of the landmarks used to identify them. Numbering corresponds to Figure 2.3.

	Morphometric	Description
1	Body length	Point of the shoulder to the most caudal point of the pin bone
2	Withers-pin length	Most caudal point of the pin bone to the highest point of the withers[a]
3	Sternum-pin length	Most caudal point of the pin bone to the sternum-barrel junction
4	Withers-knee length	Highest point of the withers to the middle of knee[a]
5	Barrel length	Highest point of the withers to the most dorsal and caudal point of the ilium[a]
6	Croup length	Most dorsal and caudal point of the ilium to the most caudal point of the pin bone
7	Barrel depth	Middle of the back to the lowest point of the barrel
8	Heart depth	Point of inflection caudal to withers to the sternum-barrel junction
9	Withers-chest depth	Highest point of the withers to sternum-barrel junction[a]
10	Forequarters depth	Point of the shoulder to the highest point of the withers[a]
11	Tibia length	Stifle to the middle of the hock
12	Forelimb cannon length	Middle of the knee to the middle of the fetlock
13	Hindlimb cannon length	Middle of the hock to the middle of the fetlock

[a] If several spinous processes are equally high at withers, use most caudal process.

Table 2.3. Summary of linear regressions comparing hand-measurements and photogrammetric estimates for each morphometric taken from domestic Newfoundland ponies near Radisson, Saskatchewan, Canada, in October, 2013. The results for tibia length are presented with four potentially influential observations removed (where $n = 26$ below) and included (where $n = 30$) to show their effect on the model parameters.

Morphometric	***n***	**Slope**	**SE**	R^2	***P* <**
Body length	30	1.136	0.007	0.999	0.001
Withers-pin length	30	1.185	0.005	1.000	0.001
Sternum-pin length	30	1.259	0.007	0.999	0.001
Withers-knee length	30	1.141	0.006	0.999	0.001
Barrel length	30	1.129	0.008	0.998	0.001
Croup length	30	1.119	0.009	0.998	0.001
Barrel depth	30	1.678	0.010	0.999	0.001
Heart depth	30	1.463	0.010	0.999	0.001
Withers-chest depth	30	1.332	0.009	0.999	0.001
Forequarters depth	30	1.155	0.007	0.999	0.001
Tibia length	26	1.155	0.009	0.999	0.001
Tibia length	30	1.140	0.014	0.996	0.001
Forelimb cannon length	30	1.000	0.009	0.998	0.001
Hindlimb cannon length	26	1.061	0.006	0.999	0.001

Table 2.4. Candidate models explaining variation in weight with hand-measurements for domestic Newfoundland ponies near Radisson, Saskatchewan, Canada, in October 2013. Predictor variables included heart depth (HD), sternum-pin length (SPL), withers-knee length (WKL), forelimb cannon length (FCL) and tibia length (TL). Models developed by stepwise backward-elimination model selection. Numerical subscripts denote which step of model selection produced the model. M_0 is the global model, M_2 is the selected model. M_{photo} was not part of the model selection. It included the photogrammetric estimates that are analogous to the hand-measurements in the selected model. M_{photo} is presented to compare the photogrammetric estimates' ability to explain variation in weight with hand-measurements (M_2). Degrees of freedom (*df*), log-likelihood (logLik), AIC_c, ΔAIC_c, and Akaike weight (*w*) reported for candidate models. Models are listed by AIC_c. ΔAIC_c is the difference in AIC_c between M_i and the model with the lowest AIC_c (i.e. M_2).

Model	**Predictor variables**	***df***	**logLik**	**AIC_c**	**ΔAIC_c**	***w***
M_2	HD + SPL + WKL	5	−112.92	238.34	0	0.51
M_1	HD + SPL + WKL + FCL	6	−111.72	239.09	0.75	0.35
M_0	HD + SPL + WKL + FCL + TL	7	−111.47	242.03	3.69	0.08
M_3	HD + SPL	4	−116.59	242.78	4.44	0.06
M_{photo}	HD + SPL + WKL	5	−132.67	277.80	39.46	

3.0 THE REPRODUCTIVE ECOLOGY OF FEMALE FERAL HORSES (*Equus ferus caballus*) ON SABLE ISLAND, NOVA SCOTIA

3.1 Introduction

Reproductive rates of large mammals can show high variation within a population (Green and Rothstein 1991; Sand 1996). Long-term studies of individually identifiable animals, such as that being undertaken on Sable Island, are conducive to the study of factors that produce variation in individual reproductive success (Gaillard et al. 2000a). It is relatively easy to study individual reproductive success for large female mammals (Gaillard et al. 2000b); however, the definition of 'reproductive success' in the literature is ambiguous as it has been used as a general term for many fitness variables (e.g., birth rate, Stokes et al. 2003; death rate from birth to one year, Cameron et al. 2009; production of an offspring surviving to weaning, Gaillard et al. 2000a). Hereafter, the term 'reproductive success' is only used when referring to the production of an offspring surviving to weaning (i.e., independence).

Reproductive output is density-dependent in several species including horses (Berger 1986; Gaillard et al. 2000b). Density-dependent effects on reproductive output may be difficult to detect: stochastic factors such as weather can obscure its influence and lag times can be long for large-bodied mammals (Berger 1986). Large-bodied mammals are generally considered capital breeders (Stearns 1992). Fat reserves supplement grazing in supplying enough energy for fetal development during gestation (Festa-Bianchet et al. 1998; Gaillard et al. 2000a) and lactation following parturition (Berger 1986; Duncan 1992). When resource limitation drives energy intake below expenditure, individuals will lose somatic fat reserves (Rudman and Keiper

1991). Thus, density-dependent effects are commonly attributed to competition for resources (e.g., Festa-Bianchet et al. 1998).

Body size of large mammals is often measured in ecological studies because of its correlation with components of an individual's fitness (Bergeron 2007). Body size is commonly represented by mass or weight, which encompasses skeletal size, muscle mass and fat reserves (Festa-Bianchet et al. 1998). Numerous studies have examined how female body size affects reproductive output, yielding mixed results (see Albon et al. 1983; Berger 1986; Green and Rothstein 1991; Duncan 1992; Cameron et al. 1993; Sand 1996; Gaillard et al. 2000a). This may be due to differences in the physiology and life histories amongst the species studied and the various biotic and abiotic conditions where they live (Festa-Bianchet et al. 1998). Nutritional stress from resource limitation for some period during the year is one of the main factors linked to female body size-fitness relationships that may be overlooked (Duncan 1992; Festa-Bianchet et al. 1998). Inadequate resources force individuals to draw energy from fat reserves for somatic growth and maintenance, or gestation and lactation (Duncan 1992); therefore, a relationship between body size and reproductive output may not be present when resources are sufficient to cover these energetic demands year-round or to allow adequate accumulation of fat reserves for harsher months, even by relatively small or lean individuals.

The best supporting evidence for relationships between body size and reproductive output often involve populations that experience long periods with poor forage, or show stronger relationships as population density increases or habitat quality declines, supporting the idea that resource limitation plays an important role (Albon et al. 1983; Cameron et al. 1993; Sand 1996; Festa-Bianchet et al. 1998). In addition, age can further confound the situation. Berger (1986) reported that body size of mature mares was positively correlated with fecundity when they had a

poorer quality home range, while Duncan (1992) found small body size resulted in reduced fecundity at peak density for immature mares but not mature mares. Hence, body size may be a determinant of reproductive output, but its influence appears to depend on the degree of resource limitation and sometimes age.

In large-bodied mammals, reproductive output for females generally increases from the age of sexual maturity to the prime-age class (Festa-Bianchet 1988); however, with abundant nutrition, young females may be as fecund as prime-age females (Gaillard et al. 2000b). Prime-age females are adults that have not begun survival senescence (Gaillard et al. 2000b) and may encompass individuals from as young as four years old (Welsh 1975) to females in their mid to late teens for feral horses (Berger 1986; Garrott et al. 1991). Age-specific reproductive rates reach their highest levels for mares at around five years of age (Berger 1986; Garrott et al. 1991) and may remain high throughout life (Welsh 1975); however, reproductive senescence may cause a gradual decline in reproductive output for the oldest mares (Garrott et al. 1991). Although reproductive rates for large bodied, prime-age female ungulates do not vary much with age within a year (Berger 1986; Festa-Bianchet 1988), the average reproductive rates of prime-age females may vary between years (Garrott et al. 1991). Age-specific fecundity may be affected by weather, density, environmental quality (Gaillard et al. 2000b) and body mass (Green and Rothstein 1991; Gaillard et al. 1992); although, the effect is generally reduced or non-existent for prime-age females (Gaillard et al. 2000b).

Since the reproductive output of young females is low at sexual maturity and increases with age, many individuals may not reproduce the first year they are sexually mature and some may not reproduce until they are adults (e.g., Green and Rothstein 1991). Early reproductive efforts can be costly for large mammals. Costs of early reproductive effort can manifest through

reductions in subsequent reproductive output. Lower fecundity for the youngest breeding females immediately following the year of primiparity was reported for Japanese serow (*Capricornus crispus*, Miura et al. 1987), bison (*Bison bison,* Green and Rothstein 1991) and northern elephant seals (*Mirounga angustirostris*, Huber 1987). Despite the temporary reduction in fecundity, the youngest breeding females had intermediate (Japanese serow) or the highest (bison) reproductive rates as adults, while the latest producing females had the lowest rates and were sometimes completely barren throughout their remaining reproductive years (Miura et al. 1987; Green and Rothstein 1991). Thus early reproductive efforts may have short-term costs, but delayed primiparity may be an indication of poor quality. Festa-Bianchet et al. (1995) observed a temporary decrease in fecundity for early producing bighorn ewes only when the population was at high density and age of primiparity did not affect lifetime reproductive output. Therefore costs may be density-dependent for some species, making them more difficult to detect. Early reproductive efforts for female feral horses generally do not occur until an individual disperses from their natal band (Welsh 1975; Berger 1986). This is a result of their social system and inbreeding avoidance behaviour: stallions rarely mate with females that matured sexually in their band (Welsh 1975; Berger 1986; Berger and Cunningham 1987). In horses, familiarity is suggested to prevent sexual activity between young sexually mature females and their fathers (Berger 1986; Berger and Cunningham 1987) and it has also been implicated in the inbreeding avoidance behaviour of primates that exhibit a similar social system (Pusey 1980).

The social system of feral horses can also affect the reproductive output of mares due to consort relationship stability (Rubenstein 1986; Kaseda et al. 1995) and the number of stallions in a band—referred to from here on as band structure (Linklater et al. 1999). Changes in stability of consort relations and band structure can arise by several means such as intergroup movement

of mares, bachelors establishing rank as subordinate males in a family band, death of a band stallion, or band takeover by bachelors or tag stallions (Berger 1983; Franke Stevens 1990; Goodloe et al. 2000; Cameron et al. 2009). Band structure can affect levels of male aggression towards mares (Linklater et al. 1999) and inter-band movement of mares can result in aggression between mares (Rutberg and Greenberg 1990; Linklater et al. 1999). Aggression towards female horses has potential negative effects on their reproductive output (Linklater et al. 1999; Cameron et al. 2009) and body condition (Linklater et al. 1999). Stallions associating with unfamiliar mares will also force them to copulate, which can cause a mare to abort a gestating fetus (Berger 1986). This feticidal behaviour is commonly observed with equids (e.g., Berger 1986; Pluháček and Bartoš 2000) and is believed to have evolved as a result of their social system (Berger 1983; van Schaik and Kappeler 1997). Infanticidal behaviour, the postnatal killing of dependent offspring (Berger 1986; Pluháček and Bartoš 2005), has evolved as a reproductive strategy in carnivores (Packer and Pusey 1983) and primates (Hrdy 1979) for the same reason as feticide in horses—to reduce the inter-birth interval (Hrdy 1979; van Schaik and Kappeler 1997). Infanticidal behaviour in feral horses has been reported (e.g., Gray 2009); however, it is a rare cause of foal mortality and its use as a reproductive strategy by horses is controversial (see Berger 1986; Gray 2009).

In large mammals like feral horses, the majority of offspring mortality occurs within one year of birth, and is concentrated within the first month (Welsh 1975; Berger 1986; Duncan 1992; Monard et al. 1997; Goodloe et al. 2000). Foals that survive to weaning, typically one year of age, are expected to live longer (Welsh 1975) and as a result will more likely have offspring of their own. Therefore, factors affecting offspring survival in the first year of life are as important to consider as factors affecting conception and gestation.

Early survival of young offspring is generally divided into pre- and postweaning survival. Preweaning survival is largely dependent on maternal care, whereas care-independent factors are the main determinants of postweaning survival (Gaillard et al. 2000b). The offspring of young as well as very old mothers may have lighter birth masses than prime-age females (Clutton-Brock et al. 1992; Duncan 1992; Festa-Bianchet et al. 1995); survival of neonates is positively correlated with birth mass and density can augment this relationship (see Albon et al. 1987; Clutton-Brock et al. 1987; Skogland 1990; Clutton-Brock et al. 1992; Cameron et al. 1993; Gaillard et al. 1997; Forchhammer et al. 2001). Additionally, younger mothers often have later parturition dates, reducing the time for young to forage and gain mass prior to winter in temperate climates (Festa-Bianchet 1988; Clutton-Brock et al. 1992; Duncan 1992). Hence, many studies have reported lower offspring survival for younger mothers (Huber 1987; Festa-Bianchet 1988; Duncan 1992; Lunn et al. 1994; Cameron et al. 2000). Postweaning mortality is often a result of inadequate nutrition (Gaillard et al. 2000b), so density (Skogland 1990; Festa-Bianchet et al. 1998) and weather (Singer et al. 1997; Portier et al. 1998) are often reported as causes.

Reproductive experience of mothers may also affect offspring survival. Cameron et al. (2000) reported that older mares actively tended more to foals in the first 20 days following parturition when foals were most likely to die and had lower preweaning mortality than younger mares. Younger and middle-aged mares that had experienced the loss of a foal also increased their effort during the first 20 days following parturition for subsequent pregnancies, as observed for older mares, reducing neonatal mortality. Similarly, Berger (1986) observed that almost all foals that died within the first month of life were born to inexperienced mothers that had never foaled previously.

I had several objectives that examined the effect of various factors on the reproductive success of female horses on Sable Island. Specifically my objectives were to determine if: 1) weather conditions (NAO index) during winter following conception and/or parturition affect the probability of age-specific reproductive success; 2) age interacts with density and/or body mass (i.e. condition) at conception or parturition to affect the probability of reproductive success; 3) body condition at conception and skeletal size of adult females may interact to affect the probability of reproductive success; 4) density at conception or parturition has a direct negative influence on the probability of reproductive success; 5) a female's reproductive experience (i.e. number of foals a female has had previously) will influence their probability of reproductive success; 6) individuals that first reproduce as sub-adults will have a lower probability of reproductive success the subsequent year than individuals that first reproduce as adults; 7) stability of consort relations and band structure at conception and parturition will affect the probability of reproductive success.

3.2 Methods

3.2.1 Study site

Sable Island National Park Reserve (43°55' N, 60°00' W) is a crescent-shaped sand bar in the Atlantic Ocean on the eastern North American continental shelf. It lies approximately 160 km from Canso Head (the nearest point on the mainland coast of Nova Scotia), and 275 km from Halifax. The island has a temperate oceanic climate (Contasti 2011) with cool summers and wet winters (van Beest et al. 2014). Average daily temperatures range from 17.8°C in August to

−0.3°C in January, and greater than 90% of the 1459.2 mm of average yearly precipitation is rainfall (Environment Canada 2012).

The island is approximately 49 km long and 1.25 km wide at its broadest point. Both the north and south beaches are flanked by dune chains averaging 9 to 12 m high, reaching up to 25 m in the east (Byrne and McCann 1993; 1995). Lower rolling dunes dominate the interior between the dune ridges (Stalter and Lamont 2006). A lens of fresh groundwater under the island is maintained by precipitation resulting in several fresh water ponds in the island's interior where surface depressions extend below the water table (Stalter and Lamont 2006). Ponds—which cover only 21.8 hectares of the island—are more prevalent in the west and those located closer to the beaches tend to be more brackish due to periodic flooding and sea spray (Stalter and Lamont 2006; Lucas et al. 2009; Contasti 2011). Many eastern ponds are ephemeral and horses must dig in the summer months to reach the high water table (deVilliers and Hirtle 2006; Lucas et al. 2009; Contasti 2011).

Apart from the population of feral horses, the island is home to the breeding populations of two species of seals, and several species of arthropods, insects, molluscs, and birds. Some species of fauna are endemic or of concern for conservation, the most notable being the Ipswich sparrow (*Passerculus sandwichensis princeps*), a sub-species of the Savannah Sparrow (*P. sandwichensis*), which breeds exclusively on the island (Beson 1998).

Sable Island, which is approximately 40% vegetated, has several plant communities composed of greater than 220 species of native and non-native grasses, forbs and shrubs, but no trees (de Villiers and Hirtle 2006; Stalter and Lamont 2006; Catling et al. 2009). Salt-tolerant plants such as sandwort (*Honckenya peploides*), beach pea (*Lathyrus maritimus*) and marram grass (*Ammophila breviligulata*) vegetate areas closest to the ocean (Beson 1998; de Villiers and

Hirtle 2006). The inland areas characterized by rolling dunes are vegetated with marram, marram-fescue, and marram-forb grassland communites, as well as shrub-heath and cranberry-heath communities (Catling et al. 1984). The inland pools have aquatic vegetation that varies with the salinity and depth of water (see Catling et al. 1984 for more detailed community descriptions). Bryophytes and lichens can also be found throughout the inland areas.

3.2.2 Field methods and census design

During each field season, teams of collaborators led by University of Saskatchewan personnel (see Contasti et al. 2012, 2013; Marjamäki et al. 2013; van Beest et al. 2014) conducted daily censuses that cumulatively encompass the entire island to identify all individuals that were born or deceased over the past year. Censuses were carried out every year from 2008–2013 and usually took place from late July to early September, except in 2009 when the census was conducted from late May to mid July. Parturition is strongly seasonal in wild horses and occurs between April and August for nearly all mares on Sable Island (Welsh 1975); therefore, most foals in a given cohort were born before or during this period. Individuals that were not sighted but were present in the previous year were assumed deceased since the island is a closed system. I distinguished yearling foals that had not been identified in the previous year from newborns based on their larger body size and winter coats as opposed to the birth coats of newborns and placed them in the proper year's cohort. The population has ranged from 398 individuals in 2008 to 559 in 2013. The resighting probability of the censuses was 0.994 for females and 0.992 for males from 2008–2013 (based on >20 000 locations). Each horse was sighted an average of 5 ± 2 ($\bar{x}$ ± SD) times a year, with a maximum of 17 sightings in a summer.

I divided the island into eight sampling areas based on landscape features and horse density (Fig. 3.1). The island was completely censused at least once a week during each field season. Each day, I conducted a walking census in a predetermined sampling area between 08:00 and 19:00. I located bands by sight from dune ridges. I identified individual horses based on coat colour and unique face and body markings described in field notes and a photo-identification database of all living horses. This method has been proven reliable from several studies of equids (see Berger 1986; Rutberg and Keiper 1993; Heitor et al. 2006). I recorded the position of each horse on the island accurate to within 7 m with a handheld GPS and took new digital photographs to later confirm the identity of each horse. During the 2008, 2012 and 2013 field seasons, I photographed horses with the parallel-laser standard (see Fig. 2.2) projected horizontally on the side of the body.

I aged horses in the field based on size and appearance and placed them into four age classes: foals (age 0), yearlings (age 1), sub-adults (ages 2 or 3) and adults (ages 4 and above). Field ages were shown to be generally without error through comparing field ages to that of known-aged individuals from 2008 to 2011. I grouped all adults together because many individuals were first observed as adults at the beginning of the study in 2008 and therefore could not be given a specific age.

I sexed horses by direct observation of external genitalia (Cameron et al. 1999). Sexing foals was sometimes difficult due to maternal protection and their small size (Contasti 2011). On censuses where the sex of a foal was not determined, I used digital photographs, notes on the foal's appearance and maternity information to sex the foal on a subsequent observation.

Foals remain close to their mothers for the first four weeks following parturition (Moehlman 1998; Ladewig et al. 2005) and mares only nurse their own offspring (Welsh 1975;

Feh 2005). I assigned maternity for mares observed nursing foals of the current year's cohort and yearlings of the previous year's cohort. Most of the foals on Sable Island are born from April to June, whereas the censuses generally took place from mid-July to early September. Therefore, we missed most of the early foal mortality each year or were not able to assign those foals that died before our arrival to a particular mare. To reduce bias I defined reproductive success as the production of a foal that survives to one year of age.

3.2.3 Life-history data

I measured body size remotely using the system described above in Chapter 2. I measured chest depth, withers-knee length, and sternum-pin length (see Fig. 2.3 and Table 2.2) on several photographs of the same individual that may span several days. I had identified heart depth, withers-knee length and sternum-pin length as strong indicators of overall skeletal size in domestic horses with close ancestry to Sable Island horses (see Chapter 2). For brevity, I will refer to these measurements as heart depth, height and length respectively. When replicates were available, I calculated averages of each measurement for each horse within a field season.

The photogrammetric photographs were taken with a different camera in 2008 than in 2012 and 2013. I suspected the systems might not be directly comparable due to bias inherent in each system (e.g., different lens distortion, focal length, etc.). I identified males that had measurements as adults for heart depth, height and length in 2008 and 2012–2013. I modeled the 2008 and 2012–2013 measurements for each morphometric with linear regressions forced through the origin. I adjusted the 2008 measurements for females with the slope from the appropriate regression. I compared the adjusted 2008 measurements for adult females to those

from 2012–2013. I found no significant difference for heart depth (Paired *t*-test, $t = -1.628$, $df = 32$, $P = 0.113$) or height (Paired *t*-test, $t = -0.411$, $df = 23$, $P = 0.685$), however length still varied between 2008 and 2012–2013 (Paired *t*-test, $t = -3.643$, $df = 27$, $P = 0.001$). This is likely a result of parallax error. My lasers were separated horizontally on the parallel-laser standard. When an individual is not square to the camera, measurements with a horizontal component will measure shorter than their true measurement. I tried to only measure photos where the horses were square to the camera, but observer error can occur. The significant difference in length between years after adjustment suggests that parallax error was more common in 2008, causing the measurements to be shorter in general. Heart depth and height did not vary significantly after adjustment because they have very little horizontal component, so parallax error did not significantly affect them.

Body growth is asymptotic in mammals; when I took measurements for an individual as an adult, I extrapolated them to others years when that individual was an adult but no measurement data were available. When heart depth and height data were available for individuals as adults in 2008 and 2012–2013, I used the 2012–2013 measurement data for years 2009–2011. Although length measurements in 2008 tended to be shorter, length measurements from 2012 were shorter for many females. When a female had length data for both years and there was a considerable difference between the values, I used the longer measurement because I assumed the shorter measurement was caused by parallax error.

I scored the body condition from census photographs as outlined by Carroll and Huntington (1988) for each female two years or older at each observation from 2008–2012. I assessed body condition scores from photographs taken between May 22 and September 9 depending on the year. The 2009 field season ran from May 22 to July 22, whereas the other

field seasons were between July 20 and September 9. I suspected that the body condition scores for 2009 would be low since the horses had not had as much time to accumulate fat following winter as in other years, and that condition scores taken earlier in a season would be lower than those taken later in the same seasons. Body condition scores increased significantly with day (GLMM, $F_{1,1821} = 11.708$, $P < 0.001$), however the estimated β was very small (0.002). Body condition did vary between years (GLMM, $F_{4,1818} = 5.757$, $P < 0.001$). A Tukey comparison revealed 2009 body condition scores were only significantly lower than those of 2011, which were also significantly higher than all other years (Table 3.1). If I shifted the condition scores to reflect the same date for all years, the change in an individual score would be 0.2 at most. Because condition was scored in half point gradations (i.e. 0.5 unit steps), I decided the effect of shifting the scores would be minimal and left the data as they were recorded. When more than one condition score was recorded for an individual in a given year, I gave that horse an average condition score for that year.

I calculated yearly median locations as the median latitudinal and longitudinal co-ordinates for each individual in each year from 2008–2012. Sable Island curves south between the east and west tips, which causes some median locations to be in the Atlantic Ocean north of the island. If an individual's median location fell off the island, I assigned it to the point of nearest landfall.

For each possible reproductive attempt (each year from 2008–2012) of each female, I determined age class in the year of parturition (age), yearly reproductive success for the year of parturition (YRS), body condition score in the summer of conception (BCS_c) and summer of parturition (BCS_p), NAO index the winter following conception (NAO_c) and following parturition (NAO_p), local density in the summer of conception ($density_c$) and summer of

parturition ($density_p$), parity status in the summer of conception ($parity_c$), band structure in the summer of conception ($structure_c$) and summer of parturition ($structure_p$), stability of consort relationships in the year prior to conception ($stability_c$) and from conception until parturition ($stability_p$) from census data. I also determined the age of primiparity ($parity_{age}$) for females first sighted prior to sexual maturity (see variable descriptions in Appendix A).

3.2.4 Statistical analyses

Using potential predictive variables identified above, I constructed a series of *a priori* predictive models to evaluate relationships affecting reproductive success (Table 3.2). Each model was not directly comparable, and reflected expected relationships as discussed in the objectives of my chapter introduction. To test if my *a priori* models influenced probability of reproductive success, I constructed generalized linear mixed effects models (GLMM) with binomial error distribution using the R Version 3.0.3 statistical software (R Core Team 2013). Only two females classified as two-year-olds at the time of parturition foaled, both in 2008. These age classifications were suspect and no other two-year-old mares gave birth in the following five years when ages for young mares were known. As a result, I only included females that were three years or older at the time of parturition in all analyses. Individual females often had data entries over several different years, causing the data to be non-independent. I incorporated year and horse ID in models as random factors to account for pseudoreplication. When $N_{obs} = N_{indiv}$ (see Table 3.2), year was the only random factor I incorporated into that model because each observation corresponded to a unique individual. Since I was testing relationships found in other

ungulates and feral horse populations, the models were set up, and each interaction and main effect was evaluated for significance against the threshold $\alpha = 0.05$.

Age has a strong influence on the reproductive output of large mammals, so I analyzed the relationship between YRS and reproductive experience ($M_{RE\text{-}x}$) or socio-ecological variables ($M_{SEC\text{-}x}$ and $M_{SEP\text{-}x}$) with different groups of individuals based on age class as designated by the subscript "-*x*". These groupings were all sexually mature females, sub-adult females, and adult females (-*All*, -*Subadult*, and -*Adult* respectively).

I only included data for adult females for model M_{SIZE} because very few body size data were available for sub-adults. Photogrammetric photographs were only taken in 2008, 2012, and 2013 and sub-adult size data could not be extrapolated to the other years since females were still growing. $M_{DENSITY}$ also only included adult data so that age effects would not confound the analysis.

I divided the effects of socio-ecological variables into two periods. Stability of consort relations the year prior to conception and band structure in the summer of conception had the potential to affect the probability of conception and were included in $M_{SEC\text{-}x}$ models. Stability of consort relations from conception until parturition and band structure in the summer of parturition had the potential to affect the probability of parturition and were included in $M_{SEP\text{-}x}$ models.

I used predicted probabilities of yearly reproductive success ($Pr(\text{success})$) for significant relationships to calculate odds ratios; the odds ratios can be used as an overall measure of effect size (Haddock et al. 1998). I calculated the odds and odds ratios according to the methods shown in Haddock et al. (1998). I calculated odds for each category of categorical explanatory

variables, or for the highest and lowest recorded value of continuous explanatory variables. I calculated the odds (Ω_x) as:

$$\Omega_x = \frac{Pr(\text{success})}{1 - Pr(\text{success})} = \frac{Pr(\text{success})}{Pr(\text{failure})}$$

Then I calculated the odds ratio (ω_i) of the more likely outcome to the less likely outcome as:

$$\omega_i = \frac{\Omega_{higher}}{\Omega_{lower}}$$

3.3 Results

The interaction between age and the NAO index in the winter following conception approached $\alpha = 0.05$ (Table 3.3). Female age was significantly related to the probability of yearly reproductive success (Table 3.3). Adult females have higher yearly reproductive success than sub-adults (Fig. 3.2). The odds that adult females will successfully reproduce are 2.09 times greater than sub-adults.

Model M_{ENERGY} had one significant interaction and no significant main effects not included in that interaction. The interaction between age and body condition in the summer of parturition was significantly correlated with the probability of yearly reproductive success (Table 3.4). For all ages the probability of yearly reproductive success decreases with increasing body condition in the summer of parturition, but the rate of decline is more gradual for adult females compared to sub-adult females (Fig. 3.3). The odds adult females with a $BCS_p = 1$ would successfully reproduce were 6.50 times greater than adult females with a $BCS_p = 4$. The odds sub-adult females with a $BCS_p = 1$ would successfully reproduce were 1178.02 times greater than sub-adult females with a $BCS_p = 4$. The odds sub-adult females with a $BCS_p = 1$ would

successfully reproduce were 9.70 times greater than adult females with a $BCS_p = 1$. The odds adult females with a $BCS_p = 4$ would successfully reproduce were 18.67 times greater than sub-adult females with a $BCS_p = 4$.

Model M_{SIZE} had one significant main effect but no significant interactions. Body condition in the summer of conception was positively correlated with the probability of yearly reproductive success (Table 3.5, Fig. 3.4). The odds adult females with a $BCS_c = 4$ would successfully reproduce were 3.76 times greater than adult females with a $BCS_c = 0.67$. Heart depth and height approached significance—heart depth being very close to the threshold α (Table 3.5).

Local exposure to density in the year of conception was negatively correlated with the probability of yearly reproductive success for adult mares (GLMM, $\beta = -0.022$, SE = 0.009, Type II Wald $X^2 = 5.74$, $df = 1$, $P = 0.017$; Fig. 3.5) and local exposure to density in the year of parturition is positively correlated with the probability of yearly reproductive success for adults mares (GLMM, $\beta = 0.026$, SE = 0.010, Type II Wald $X^2 = 7.54$, $df = 1$, $P = 0.006$; Fig. 3.6). The odds adult females with $density_c = 11.47$ would successfully reproduce were 4.21 times greater than adult females with $density_c = 75.49$. The odds adult females with $density_p = 75.49$ would successfully reproduce were 5.31 times greater than adult females with $density_p = 11.47$.

When all age classes were included (i.e., model $M_{RE\text{-}All}$), the probability of yearly reproductive success in relation to previous reproductive experience (i.e., parity status in the summer of conception) approached significance (GLMM, Type II Wald $X^2 = 5.36$, $df = 2$, $P = 0.069$). All sub-adults were nulliparous prior to conception and had low reproductive success (35/96=36.5%) so an age effect may have been the cause of this trend. The yearly reproductive success of adult mares was similar regardless of parity status in the summer of conception

(nulliparous: 29/62=46.8%; primiparous: 40/79=50.6%; multiparous: 100/195=51.3%) and previous reproductive experience had no influence on the probability of yearly reproductive success (GLMM, Type II Wald X^2 = 0.398, *df* = 2, *P* = 0.820).

Females that first reproduced as sub-adults and females that first reproduced as adults did not vary significantly in their probability of reproductive success the year following primiparity (GLMM, Type II Wald X^2 = 3.04, *df* = 1, *P* = 0.081).

For adults or sub-adults, the probability of yearly reproductive success was not significantly related to the stability of consort relations the year prior to conception (adults: GLMM, Type II Wald X^2 = 0.755, *df* = 1, *P* = 0.385; sub-adults: GLMM, Type II Wald X^2 = 0.005, *df* = 1, *P* = 0.942), band structure in the summer of conception (adults: GLMM, Type II Wald X^2 = 0.176, *df* = 1, *P* = 0.675; sub-adults: GLMM, Type II Wald X^2 = 1.22, *df* = 1, *P* = 0.269) or band structure in the summer of parturition (adults: GLMM, Type II Wald X^2 = 1.44, *df* = 1, *P* = 0.230; sub-adults: GLMM, Type II Wald X^2 = 0.435, *df* = 1, *P* = 0.510). The probability of yearly reproductive success was significantly related to stability of consort relations from conception until parturition for adults (GLMM, Type II Wald X^2 = 13.94, *df* = 1, *P* < 0.001; Fig. 3.7) but not sub-adults (GLMM, Type II Wald X^2 = 0.620, *df* = 1, *P* = 0.431). The odds adult females in stable consort relationships from conception until parturition would successfully reproduce were 2.12 times greater than adult females in unstable consort relationships.

3.4 Discussion

I found that sub-adults had lower yearly reproductive success than adult females, which is very common in large-bodied mammals (Gaillard et al. 2000b). For horses, reproductive output usually increases from sexual maturity until around five years of age (Berger 1986; Garrott et al. 1991). My adult age class included prime-age and senescent adults; the difference between sub-adult and prime-age females is likely greater than the difference between age classes I present here. The difference in reproductive success between age classes could be a result of several factors such as reaching a threshold size (Duncan 1992), detection of estrous by a male willing to mate (Kaseda et al. 1995) or reproductive experience (Berger 1986).

Cameron et al. (2000) and Berger (1986) noted that inexperience affected reproductive output in different populations of feral horses. However, Cameron et al. (2000) included three-year olds and Berger (1986) noted inexperience was a result of young age. The differences in reproductive output due to age may confound the analysis of reproductive experience when not accounted for because younger females are generally less experienced. On Sable Island, average yearly reproductive success for sub-adults was low (36.5%), and all sub-adults were previously nulliparous. Yearly reproductive success was approximately 50% for adults regardless of previous reproductive experience. Thus when potential effects of age are removed reproductive experience does not affect reproductive success for Sable Island horses.

Early reproductive efforts may result in a subsequent short-term reduction in reproductive output for large-bodied mammals (e.g., Green and Rothstein 1991); however, I did not detect any short-term reproductive costs related to age of primiparity on Sable Island. This may be due in part to the somewhat short time period this study encompassed, limiting the resolution of my

analysis. I could not accurately assign an exact age for a number of mares, and thus had to restrict analyses to age class. Although I could determine that early primiparity had no effect on subsequent reproductive success, the large age-range encompassed in the adult age-class prevented me from analyzing if relatively late primiparity may have an effect.

The youngest parturient mares of confirmed age on Sable Island were three-year-old sub-adults (Welsh 1975; this study). For horses living in the continental US (i.e., the Granite Range population) mares as young as two-years-old were observed with offspring (Berger 1986). Perhaps mares that are parturient at two would show a temporary decline in reproductive success in the subsequent year, as seen in other large ungulates (e.g., Miura et al. 1987; Green and Rothstein 1991). However, reproductive costs from early reproductive efforts are not seen universally across mammalian taxa and may only be evident in high density populations (e.g., Lunn et al. 1994; Festa-Bianchet et al. 1995). Therefore it is possible that no effect would be detected, even when individuals foal at two-years of age.

It is unusual that density would be both positively and negatively related to reproductive success on Sable Island depending on when reproductive effort is measured. I found density in the year of conception was negatively associated with yearly reproductive success for adults. Consistent with these results, van Beest et al. (2014) found lower finite rates of increase (i.e., λ) as density increases on Sable Island. A common causal mechanism mentioned when such a relationship is present in studies of ungulates is that forage is becoming limited as density increases (e.g., Albon et al. 1983; Festa-Bianchet et al. 1998). Sable Island horses select for high-quality grasslands when density is lower, but as population density increases, they increase their selection for low-quality heathlands (van Beest et al. 2014). This density-dependent resource selection suggests density-dependent forage limitation may be a factor on Sable Island,

particularly in winter when forage quality declines (Welsh 1975). The earliest known age of sexual maturity for females on Sable Island from this study is two years, and the reproductive output is low compared to continental US populations (e.g., Granite Range) indicating that forage is relatively limited and/or of poorer quality on Sable Island (Berger 1986). Welsh (1975) confirms that the nutritive value of Sable's forage is relatively poor compared to levels 'normally encountered in forage grasses;' however, Lucas et al. (1991) reported females were sexually mature at one-year and foaled at two-years old on Sable Island when the population size was lower than observed during this study (at most 360 individuals), suggesting density-dependent forage limitation might also be occurring.

If density is limiting forage, then how does density in the summer of parturition have a positive relationship with yearly reproductive success on Sable Island? These trends seem counter-intuitive but may be explained by the distribution of a limiting resource—water. On Sable Island, horse density is higher in the west and lower in the middle and east. The availability of water is also lower in the middle and east. Water is the main component of milk, and water deprivation can reduce the quantity and quality of milk produced by mammals (see Cain et al. 2006 and references therein). Welsh (1975) proposed that poor quality or insufficient milk could cause weakness in foals and was a potential cause of early foal mortality. Lactating mares with young foals usually initiated movement towards waterholes (Welsh 1975), further supporting the idea that water may be a limiting resource for lactating mares on Sable Island. If milk production was reduced during the first few months of life because of dry weather in the spring and summer, foals could fail to receive enough colostrum or nutrition and perish.

While precipitation during warmer months can be favourable to the horses' reproductive output, prolonged wet winter weather can have a negative effect. Despite such evidence in an

earlier report (Welsh 1975), no relationship was detected between the NAO index in winter and reproductive success in this study. The NAO is an index of the difference in normalized sea level pressures (SLP) between the Icelandic low-pressure zone measured at Stykkisholmur, Iceland and the Azores high-pressure zone which can be measured at Lisbon, Portugal; Ponta Delgada, Azores; or Gibraltar (Osborn et al. 1999; Ottersen et al. 2001). The NAO index in this analysis used Azores low SLP measured at Gibraltar. The NAO influences winter weather; strong positive NAO phases are associated with warmer and wetter than average winters and strong negative phases are associated with colder than average winters in the eastern United States (Dai et al. 1997; Notaro et al. 2006) with the potential for large snowstorms (Seager et al. 2010). The NAO index in winter varied from −2.54 to 2.08 during this study. It is possible that the change in weather conditions associated with this range in the winter NAO index was not sufficient to affect the reproductive success of female horses on Sable. In addition, winters on Sable Island are relatively mild: the coldest monthly average from December 2007 to March 2013 was −4.0°C and the lowest recorded temperature was −12.3°C (Environment Canada 2015). It seems unlikely that temperatures in this range would affect the reproductive success of the Sable Island horses since the Yakut horses (*Equus ferus caballus*) of northeastern Russia tolerate winters temperatures as low as −68°C (Solomonov et al. 2009). Welsh (1975) reported a major die-off—40% of adult mares—occurred in late winter when rainfall was followed by freezing temperatures. The high adult mortality was accompanied by a considerable increase in abortions relative to previous years and females in poor condition were more likely to abort their fetus during harsh winters (Welsh 1975). The wet winter weather associated with the NAO index is usually accompanied by warmer temperatures. Perhaps general descriptions of winter weather

such as the NAO index are unable to identify acute adverse weather events that have been associated with high mortality and abortion rates on Sable Island.

Body condition is a strong predictor of reproductive output in horses regardless of winter weather conditions (Berger 1986). I also found body condition scores influenced yearly reproductive success for female horses on Sable Island; however, skeletal size did not. Although many studies discuss the effects of 'body size' on reproductive output, most measure body mass. Body mass measures variation in both of the size components that may influence reproductive output—skeletal size and fat reserves (Festa-Bianchet et al. 1998). Inter-individual variation in body mass may be largely due to differences in skeletal size or body fat, but when measured together it can be unclear which factor is the cause (Festa-Bianchet et al. 1998). As skeletal size is not an important predictor of reproductive success for horses on Sable Island despite large inter-individual variation in each morphometric analyzed (Fig. 3.8), it seems the 'body size' relationships reported in other horses populations are mainly due to differences in fat reserves (e.g., Duncan 1992). Horses are considered capital breeders and body condition scores are correlated with reproductive output in horses (Berger 1986) further supporting this conclusion.

Capital breeders generally need high fat reserves to conceive and then catabolize those fat reserves to provide their offspring with energy throughout gestation and lactation (Berger 1986; Festa-Bianchet et al. 1998). For energy reserves to play a role in reproductive success, forage would have to be limited at higher density or for some period during the year. The decline in forage quality during the winter on Sable Island (Welsh 1975) is sufficient that fat reserves are needed to help supply energy for gestation resulting in lower BCS_p. However, reproductive effort affects BCS_p of the age classes differently. The quicker drop and greater overall range in probability of yearly reproductive success in relation to BCS_p in sub-adults relative to adults

indicate that if sub-adult females reproduce, they are very likely to be in poor condition following gestation, whereas the reproductive status of adult females is not as strong an indicator of their BCS_p.

The energy demands of adult females are much more variable than sub-adults. Both adults and sub-adults can have intestinal parasites, so parasite infestation would similarly affect both groups' energy demands (Welsh 1975). While pregnant, all sub-adults must allocate energy towards growth, whereas adult females do not need to allocate energy towards growth, but may or may not be nursing a foal (Welsh 1975; Berger 1986). In addition, previous unsuccessful reproductive attempts can still be energetically expensive, even when offspring die shortly after birth. Recent reproductive attempts may influence the body condition of adults in subsequent years (Green and Rothstein 1991) and adult mares in better/poorer condition at conception are often in better/poorer condition at parturition (Berger 1986). The highly variable energy demands of adult mares are consistent with the more gradual curve in probability of yearly reproductive success in adults versus sub-adults.

Body condition near conception is correlated with reproductive output in other horse populations, particularly when resources were limited (Berger 1986). I only detected a significant effect of BCS_c for adult females, which is unusual (see Duncan 1992). There could be a few reasons why BCS_c is not a significant predictor of reproductive success for sub-adult females. Female mammals including horses need to reach a threshold mass to reproduce for the first time (Berger 1986; Duncan 1992; Gaillard et al. 2000b). Perhaps some sub-adults have a high BCS_c during the breeding season but are still not large enough and therefore do not reproduce or conceive. Detection of estrous by males willing to mate may also be a causal factor. Young females generally move between bands more frequently and have unstable consort relations

(Salter and Hudson 1982; Goodloe et al. 2000). Therefore males may not mate them within the short period when females are receptive (Welsh 1975). Finally, behavioural factors related to their social system may be the cause as many young mares simply do not mate until they are four years old and have reached full size (Welsh 1975).

The stability of consort relations during the breeding season or gestation has been shown by other researchers to influence reproductive output (e.g., Welsh 1975; Berger 1986; Kaseda et al. 1995; Goodloe et al. 2000; Rubenstein and Nunez 2009). I also found that adult mares with unstable consort relations from conception until parturition have lower reproductive success than adult mares with stable consort relations, but there was no effect in sub-adults or when the change occurs prior to conception for either age class. In contrast to my findings, Berger (1986) and Kaseda et al. (1995) reported an effect of stability regardless of age class for feral horses in the Granite Range (USA) and Misaki Range (Japan) respectively. Mares in the Granite Range are reported to first foal at two-years of age and sub-adults (two- and/or three-year olds) from the Granite and Misaki ranges have relatively high foaling rates compared to several other feral horse populations (Berger 1986; Kaseda et al. 1995). Mares first reproduce at three years on Sable Island and sub-adults generally have lower reproductive output (see Table 3.6), which is more comparable to horse populations along the east coast of North America (see Keiper and Houpt 1984; Goodloe et al. 2000). The poor reproductive output for three-year olds on Sable Island in general potentially prevents any significant difference from being detectable.

Consort relationships can end or become unstable either by a female leaving and sometimes returning to a band or by stallion takeover (Welsh 1975; Kaseda et al. 1995). Therefore, there can be a few potential causes for this trend in adults and their validity is based on when consort relationships are unstable. Mares with unstable consort relations during the

breeding season in the Misaki Range had longer inter-birth intervals—suggesting they conceived during a later estrous cycle—and lower foaling rates (Kaseda et al. 1995). Based on observations of mating behaviour in wild equids (see Salter and Hudson 1982; Asa et al. 1979), Kaseda et al. (1995) concluded that consort stability is important during conception because the stallion must detect the optimal time for mating and therefore be close to the female. Welsh (1975) noted that all mating involving courtship took place at estrous and females were generally receptive for only one day. Such a short window of receptivity suggests that if stallions fail to detect estrous because a mare is moving between groups, she may fail to conceive during that cycle. Mares will ovulate every 13 to 28 days until conception, and some stop ovulating after 3 or 4 unsuccessful cycles (Welsh 1975). Since mares within stable bands may not conceive, even when mated (Welsh 1975), it is logical that mares moving between groups are less likely to conceive.

Females could have stable consort relationships during the breeding season and unstable relationships during the winter months (i.e., the gestation period). Stallion takeover or dispersal of pregnant females within six months of conception can result in the abortion of the fetus, while mares that disperse or experience band takeovers after six months post-conception usually carry the pregnancy to term (Berger 1983; 1986). Stallions will force unfamiliar mares to copulate and this is believed to cause the abortions (Berger 1983; 1986; Pluháček and Bartoš 2000). Berger (1986) did not observe forced copulations with some of the mares that aborted and speculated that harassment of mares in new social environments may also cause abortions, although he acknowledged that forced copulations potentially occurred when the horses were not under observation. Feticidal behaviour has been observed in several other equids, with reports of forced copulation with pregnant mares occurring in several sub-species of captive plains zebra (*Equus burchelli,* Pluháček and Bartoš 2000; Pluháček and Bartoš 2005) and Przewalski's horses (*Equus*

ferus przewalskii, Berger 1986). Captive plains zebra were also observed to abort within a few days following forced copulations with an unfamiliar stallion (Pluháček and Bartoš 2000), although some pregnancies were carried to term (Pluháček and Bartoš 2005).

Feticidal behaviour is used by male horses to decrease the time until an unfamiliar female will come into estrous (Berger 1983). Feral horses are generally considered to be seasonally polyestrous (Salter and Hudson 1982; Kirkpatrick and Turner 1986) but may come into estrous year round (e.g., Welsh 1975; Berger 1983); however very few mares come into estrous outside the spring/summer breeding season (Welsh 1975). Females that aborted due to forced copulations came into estrous within a few weeks and around half of the new stallions sired foals that survived to one year (Berger 1986). The decreased time for aborting females to come into estrous is particularly important for bachelors acquiring a band because new bands may be more unstable (Rutberg 1990). Welsh (1975) reported that of the herds that formed during his three-year study on Sable Island, 40% lasted less than six months and more than half lasted less than a year. Without feticidal behaviour, stallions that formed new consort relationships with pregnant females in the fall and early winter potentially would not have the opportunity to mate with their consort before she comes into post-partum estrous in the spring.

A similar mating strategy is observed in primates with year-round male-female associations. Male primates use infanticide, as opposed to feticide, to reduce inter-birth intervals (Watts 1989) because some primate infants develop slowly and females have long inter-birth intervals as a result (Harvey and Clutton-Brock 1985; van Schaik and Kappeler 1997). Female horses come into post-partum estrous 6 to 10 days following parturition (Welsh 1975); therefore infanticide does not shorten inter-birth intervals for horses (Berger 1986; van Schaik and Kappeler 1997) and is less common, although it still occurs for other reasons (see Berger 1986).

The female-defense polygynous mating system exhibited by feral horses and some other equids is believed to be a means of reducing feticidal behaviour (van Schaik and Kappeler 1997; Linklater et al. 1999). Males should leave females following fertilization if desertion does not reduce their reproductive success (Maynard Smith 1977). Therefore, mares without stable year-round consort relationships during gestation have reduced reproductive success and it is beneficial for a stallion to protect his harem throughout the year.

I did not see a difference in yearly reproductive success due to band structure at conception or parturition. In the Kaimanawa feral horse population in New Zealand, Linklater et al. (1999) observed greater mortality from pregnancy detection to one year for multi-stallion mares than single-stallion mares, whereas Cameron et al. (2003; 2009) reported no difference in offspring survival from birth to one-year between these band types. Cameron et al. (2009) and Linklater et al. (1999) reported mares in single-stallion bands had higher foaling rates than mares in multi-stallion bands, whereas Cameron et al. (2003) reported no difference in foaling rate. Although they studied the same population, Cameron et al.'s (2003) results on foaling rates differed from Linklater et al. (1999) and Cameron et al. (2009), but in general, mares in single-stallion bands were more likely to foal.

None of these measurements—which are actually foaling rates or fetus and/or foal survival rates—are equivalent to my measurement of reproductive success. The inconsistent conclusions of these studies suggest that band structure might have a weak influence on reproductive output that may not always be evident. If true, other factors that are stronger determinants of reproductive output may have overshadowed the effect of band structure in my study and resulted in no significant effect.

Mares in multi-stallion bands receive more aggression from stallions due to agonistic interactions with tag stallions—which do not occur in single-stallion bands as there are no tag stallions present—and it has been suggested that this causes the difference in foaling rates in Kaimanawa (Linklater et al. 1999). Whether the different levels of aggression decrease conception or increase abortion rates is not known. Linklater et al. (1999) gives stronger support for an increase in abortions in multi-stallion bands; however, the two factors could work together to cause the difference in foaling rates. Despite the higher foaling rate in single-stallion bands, this may not translate into higher fitness since there is no difference in reproductive success between mares in single- or multi-stallion bands on Sable Island. Differences in foaling success between band types are meaningless if they are not apparent after the greatest period of offspring mortality.

Reproductive success to one-year varies due to maternal care and care-independent factors that will affect offspring survival during the first year of life, in addition to factors affecting conception and gestation. The lack of a difference in short-term reproductive success between the band types—even when maternal age is accounted for—suggests that band structure doesn't affect survival during the first year of life. Cameron et al. (2003; 2009) confirms that survival of foals to one year is not determined by band structure. This suggests maternal care or quality and/or care independent factors might be more important and differences in aggression between band types do not have short-term influences on reproductive success.

Both unstable consort relations and multi-stallion band structure increase aggression from either stallions (Linklater et al. 1999) or harem mares (Rutberg and Greenberg 1990), but stallions only force copulation with unfamiliar mares (Welsh 1975). Considering that multi-stallion mares receive more aggression than single-stallion mares but there is no short-term effect

of band structure on reproductive success, it appears aggression is not responsible for the decreased reproductive success of females immediately following dispersal or band takeover. I believe short-term effects on reproductive success due to unstable consort relationships are caused by feticidal behaviour. Aggression potentially has more long-term effects and acts by reducing condition of the female (Cameron et al. 2003), which could affect long-term reproductive output. Therefore, the effect of aggression on new mares may be negligible in the current year, but may affect them in subsequent years. Long-term effects should be explored in the future when sufficient data are available.

Figure 3.1. Map of Sable Island, Nova Scotia overlain with the eight census sampling areas. Green outlines vegetated area, tan outlines and blue outlines permanent ponds. Modified from Contasti (2011).

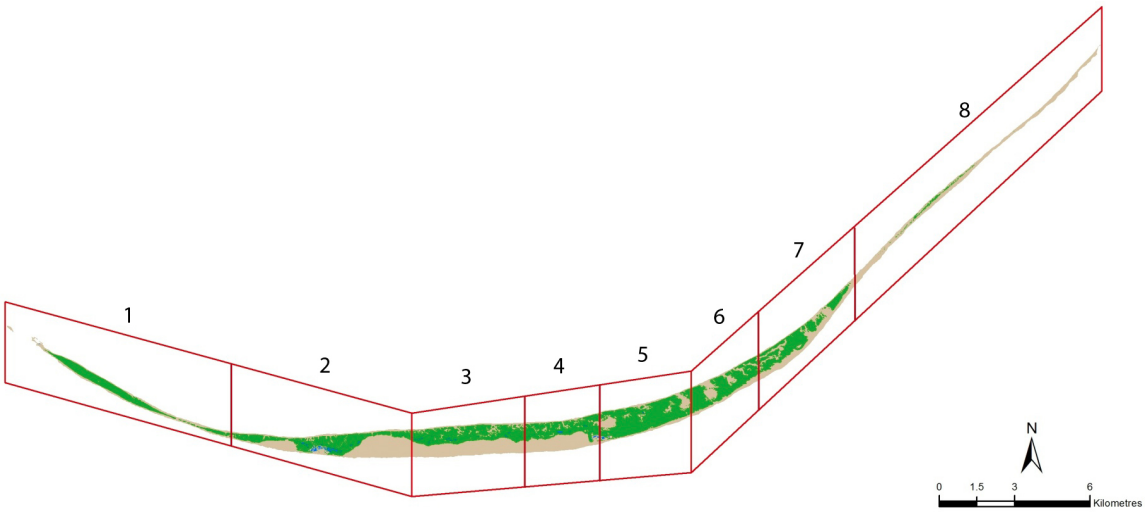

Figure 3.2. Predicted probability of yearly reproductive success of female horses on Sable Island, Nova Scotia (2009–2012) for each age class in the year of parturition based on model M_{AGE} ($\bar{x}$ ± 95% CI). I calculated yearly reproductive success for the year of parturition and defined the probability of yearly reproductive success as the probability a female will produce a foal that survives to yearling age.

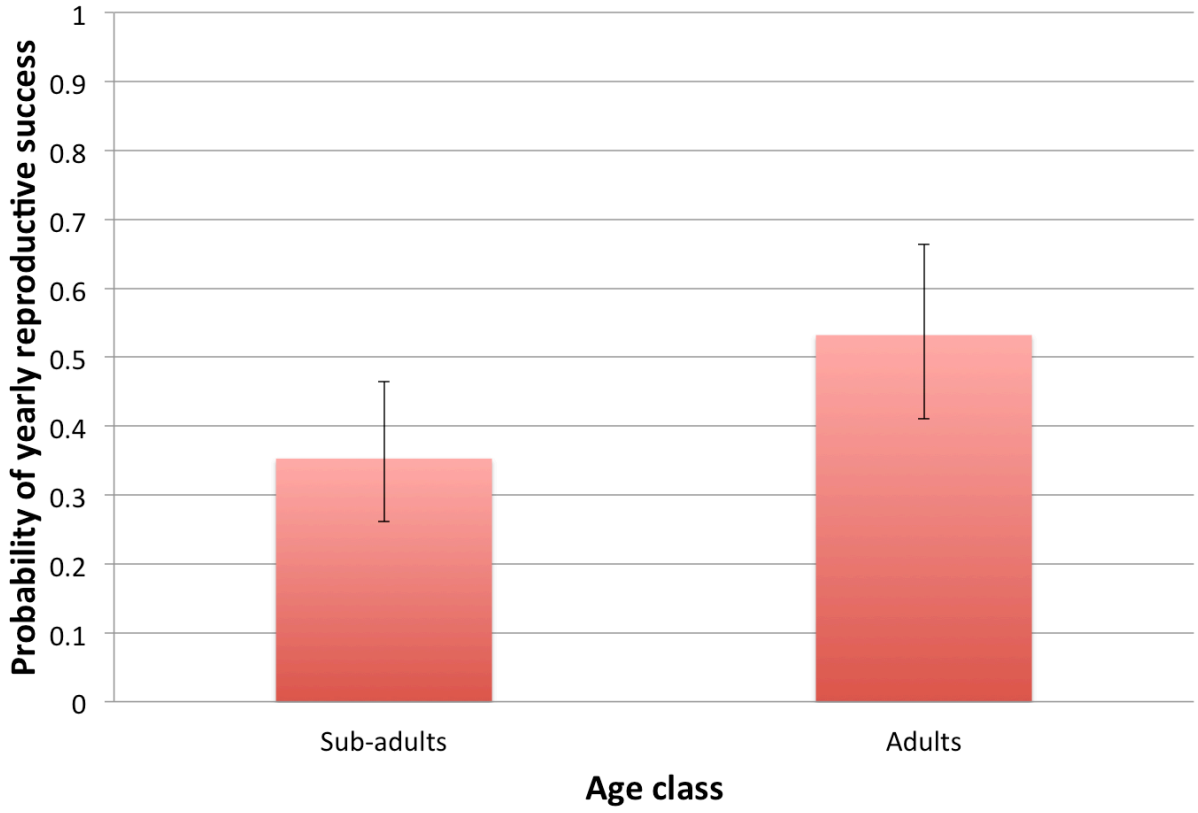

Figure 3.3. Predicted probability of yearly reproductive success of female horses on Sable Island, Nova Scotia (2009–2012) in relation to body condition in the summer of parturition for adult (ages 4 + years, red) and sub-adult (age 3 years, black) based on model M_{ENERGY}. The solid lines represent the predicted probability of reproductive success and the dashed lines represent the 95% CI of the logistic curves. I calculated yearly reproductive success for the year of parturition and defined the probability of yearly reproductive success as the probability a female will produce a foal that survives to yearling age.

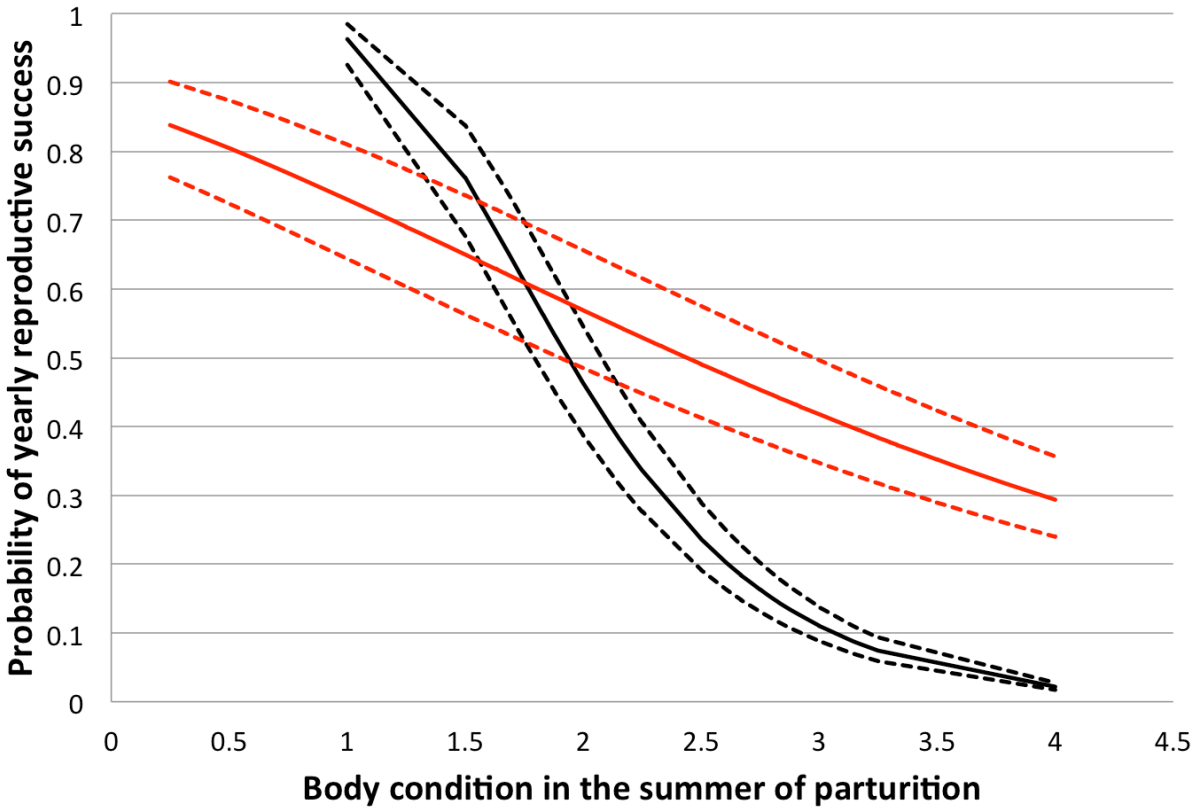

Figure 3.4. Predicted probability of yearly reproductive success of adult female horses on Sable Island, Nova Scotia (2009–2012) in relation to body condition in the summer of conception based on model M_{SIZE}. The solid line represents the predicted probability of reproductive success and the dashed lines represent the 95% CI of the logistic curve. I calculated yearly reproductive success for the year of parturition and defined the probability of yearly reproductive success as the probability a female will produce a foal that survives to yearling age.

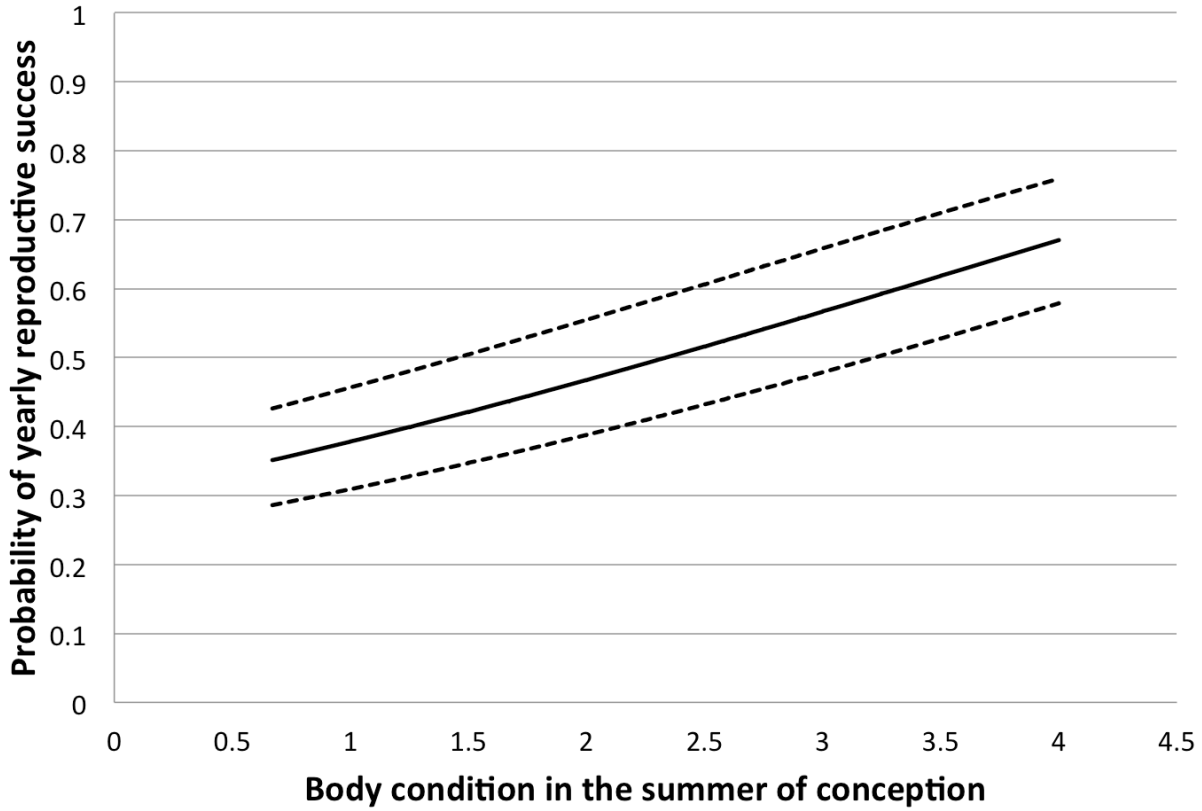

Figure 3.5. Predicted probability of yearly reproductive success of adult female horses on Sable Island, Nova Scotia (2009–2012) in relation to local density in the summer of conception based on model $M_{DENSITY}$. The solid line represents the predicted probability of reproductive success and the dashed lines represent the 95% CI of the logistic curve. I calculated yearly reproductive success for the year of parturition and defined the probability of yearly reproductive success as the probability a female will produce a foal that survives to yearling age.

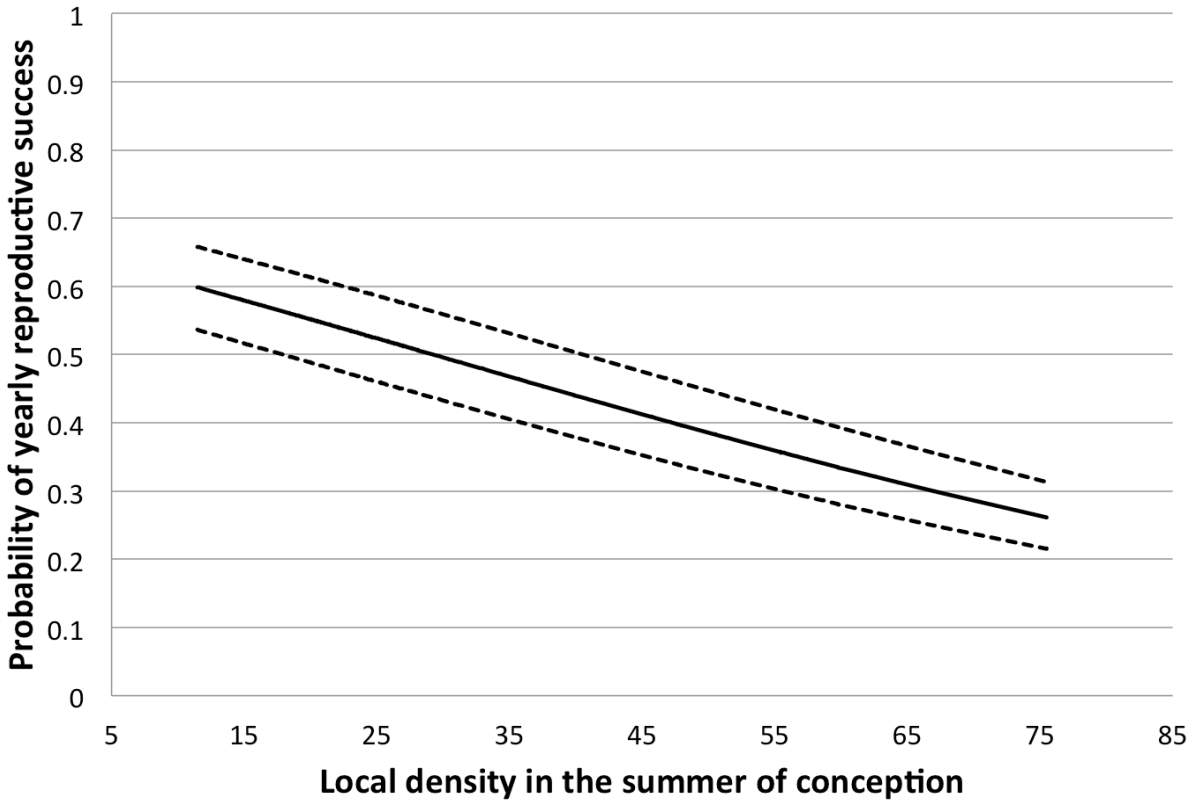

Figure 3.6. Predicted probability of yearly reproductive success of adult female horses on Sable Island, Nova Scotia (2009–2012) in relation to local density in the summer of parturition based on model $M_{DENSITY}$. The solid line represents the predicted probability of reproductive success and the dashed lines represent the 95% CI of the logistic curve. I calculated yearly reproductive success for the year of parturition and defined the probability of yearly reproductive success as the probability a female will produce a foal that survives to yearling age.

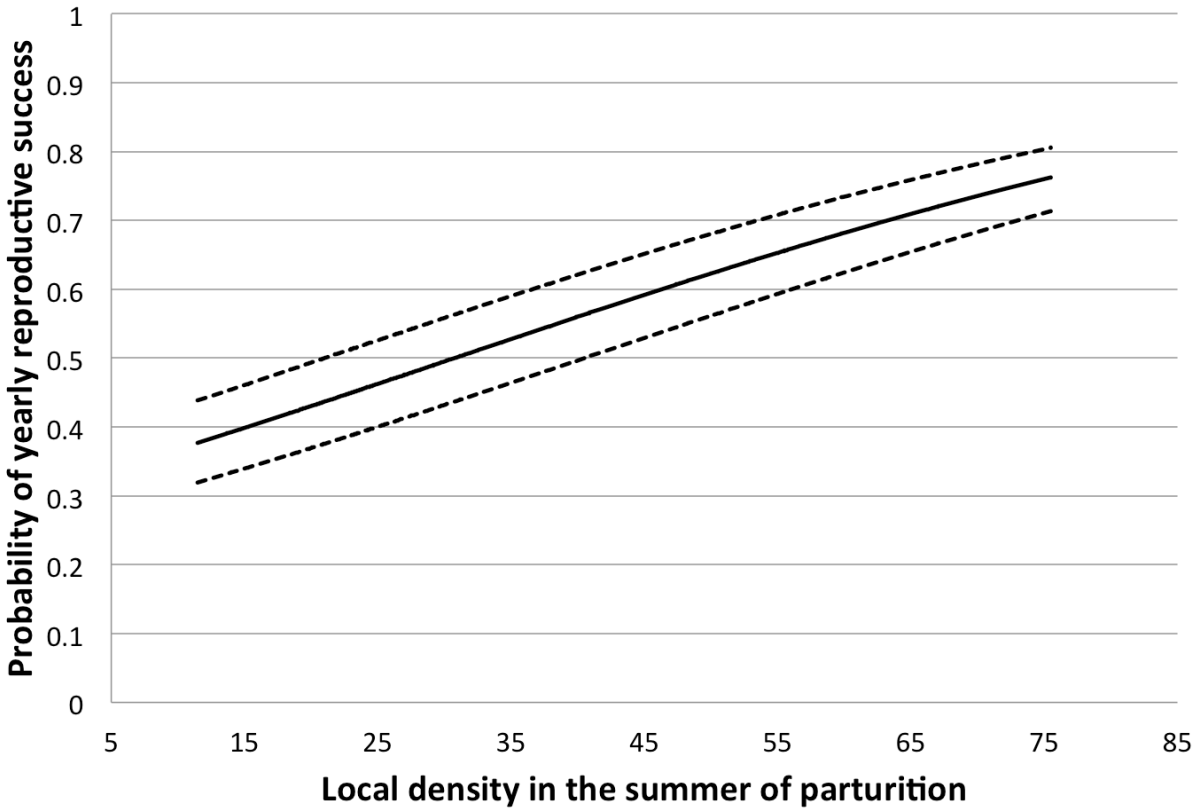

Figure 3.7. Predicted probability of yearly reproductive success of adult female horses on Sable Island, Nova Scotia (2008–2012) based on the stability of consort relationships from conception until parturition based on model $M_{SEP\text{-}Adult}$ ($\bar{x}$ ± 95% CI). I calculated yearly reproductive success for the year of parturition and defined the probability of yearly reproductive success as the probability a female will produce a foal that survives to yearling age.

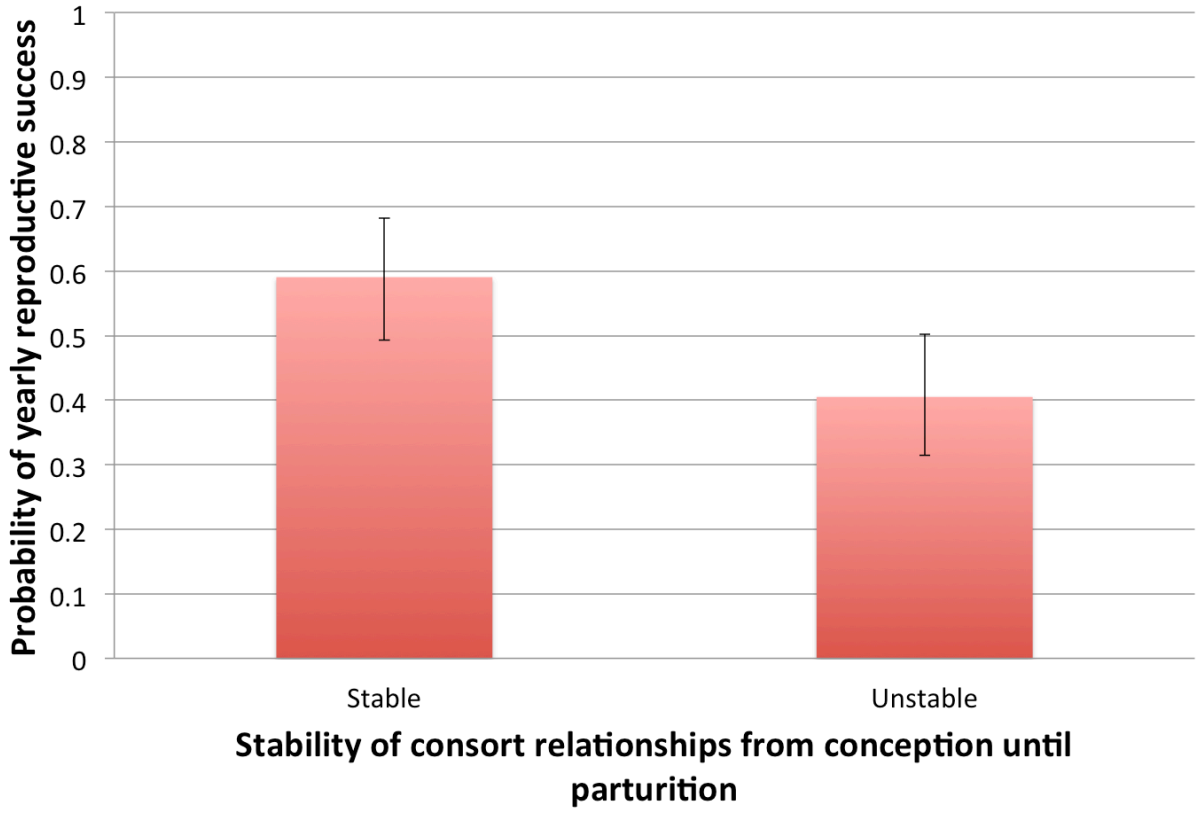

Figure 3.8. Box and whisker plots showing photogrammetric estimates of length, height and heart depth for adult female horses from Sable Island. Photogrammetric estimates were measured in centimeters from photographs taken in 2008, 2012 and 2013.

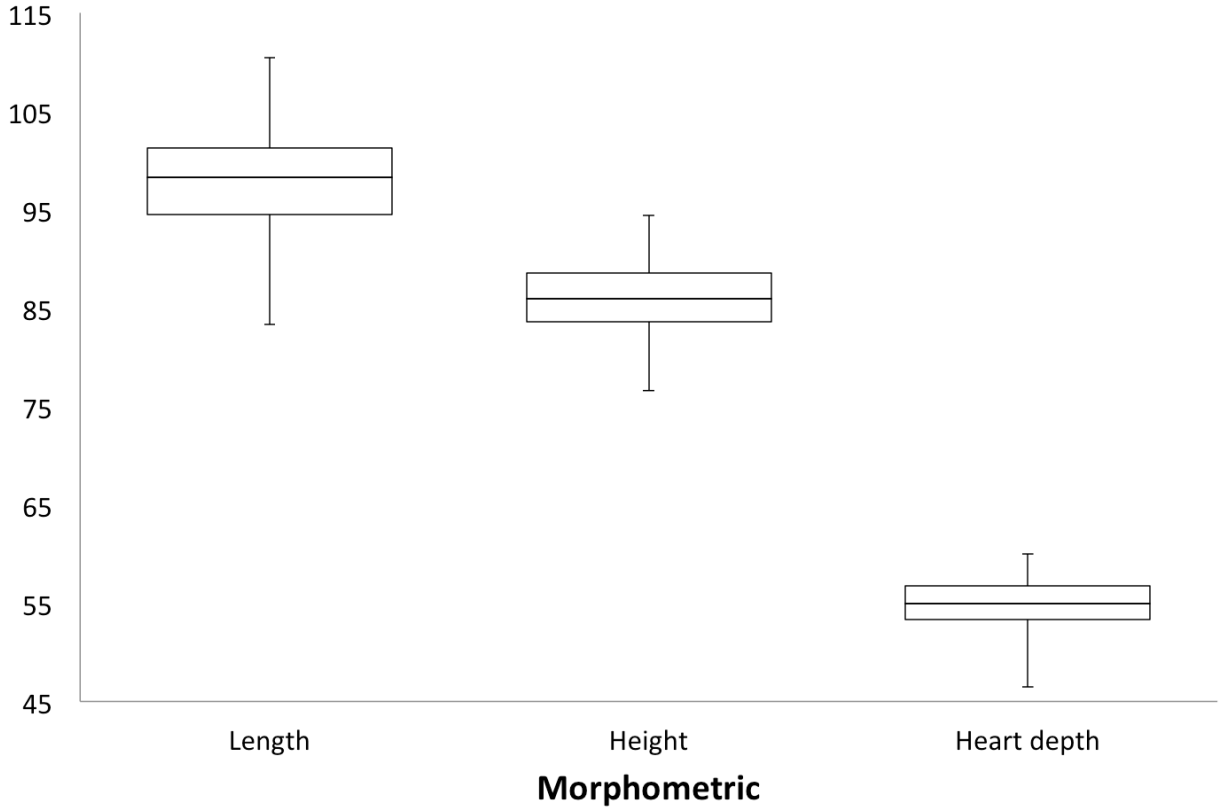

Table 3.1. Tukey multiple comparisons of means of body condition scores between years (n_{2008} = 242, n_{2009} = 342, n_{2010} = 637, n_{2011} = 385, n_{2012} = 455) for female feral horses on Sable Island, Nova Scotia from 2008–2012.

Comparison	**Difference**	***P***
2009–2008	−0.0008	1.000
2010–2008	0.1039	0.183
2011–2008	0.2450	< 0.001
2012–2008	0.1207	0.111
2010–2009	0.1047	0.093
2011–2009	0.2458	< 0.001
2012–2009	0.1215	0.053
2011–2010	0.1411	0.005
2012–2010	0.0168	0.992
2012–2011	−0.1243	0.035

Table 3.2. Model name, predictors, link function, number of observations (N_{obs}), number of individuals (N_{indiv}) and years of census data (N_{years}) for each generalized linear mixed effects models with binomial error distributions describing the probability of yearly reproductive success for mares on Sable Island, Nova Scotia. Model predictors are body condition score in the summer of conception (BCS_c) or parturition (BCS_p), NAO-index the winter following conception (NAO_c) or parturition (NAO_p), local density in the summer of conception ($density_c$) or parturition ($density_p$), parity status in the summer of conception ($parity_c$), band structure in the summer of conception ($structure_c$) or parturition ($structure_p$), stability of consort relationships in the year prior to conception ($stability_c$) or from conception until parturition ($stability_p$) and age of primiparity ($parity_{age}$). When $N_{obs} = N_{indiv}$, year was the only random factor included in that model.

Model	Model predictors[a]	Link function	N_{obs}	N_{indiv}	N_{years}
M_{AGE}	age × NAO_c + age × NAO_p	clog-log	642	194	2009–2012
M_{ENERGY}	BCS_p × $density_p$ × age + BCS_c × $density_c$ × age	clog-log	522	186	2009–2012
M_{SIZE}	BCS_c × heart depth + BCS_c × length + BCS_c × height	clog-log	378	128	2009–2012
$M_{DENSITY}$	$density_c$ + $density_p$	logit	446	162	2009–2012
$M_{RE\text{-}All}$	$parity_c$	logit	435	165	2008–2012
$M_{RE\text{-}Adult}$	$parity_c$	logit	336	140	2008–2012
$M_{PRIMIPARITY}$	$parity_{age}$	logit	58	58	2008–2012
$M_{SEC\text{-}Adult}$	$stability_c$ + $structure_c$	logit	406	161	2009–2012
$M_{SEC\text{-}Subadult}$	$stability_c$ + $structure_c$	logit	71	71	2009–2012
$M_{SEP\text{-}Adult}$	$stability_p$ + $structure_p$	logit	504	165	2008–2012
$M_{SEP\text{-}Subadult}$	$stability_p$ + $structure_p$	logit	92	92	2008–2012

[a]For all interactions, lower-order interactions and main effects of parameters are included in the model subset

Table 3.3. Analysis of yearly reproductive success for adult and sub-adult (age 3 years +) female feral horses in Sable Island, Nova Scotia in relation to age class and North Atlantic Oscillation index values during the winter following conception (NAO_c) and parturition (NAO_p) using generalized linear mixed effects models with binomial error distribution and complementary log-log link function (model M_{AGE}). Data includes 642 observations of 194 horses over 4 years (2009–2012). Horse ID and year were incorporated as random effects. Colons denote interaction terms.

Parameter	**β**	**SE**	***df***	**Wald X^2**	***P*-value**
age	0.557	0.185	1	8.041	0.005
NAO_c	−0.081	0.107	1	0.331	0.565
NAO_p	−0.134	0.114	1	1.263	0.261
age:NAO_c	0.220	0.113	1	3.762	0.052
age:NAO_p	0.062	0.123	1	0.256	0.613

Table 3.4. Analysis of yearly reproductive success for adult and sub-adult female feral horses in Sable Island, Nova Scotia in relation to age class (age), body condition score in the summer of conception (BCS_c) or parturition (BCS_p), and local density in the summer of conception ($density_c$) or parturition ($density_p$) using generalized linear mixed effects models with binomial error distribution and complementary log-log link function (model M_{ENERGY}). Data includes 522 observations of 186 horses over 4 years (2009–2012). Horse ID and year were incorporated as random effects. Colons denote interaction terms.

Parameter	**β**	**SE**	***df***	**Wald X^2**	***P*-value**
BCS_p	−1.670	0.446	1	11.245	< 0.001
$density_p$	−0.021	0.020	1	0.107	0.744
age	0.939	0.328	1	2.350	0.125
BCS_c	1.205	0.691	1	2.288	0.130
$density_c$	0.005	0.028	1	0.080	0.777
BCS_p:$density_p$	−0.033	0.034	1	0.793	0.373
BCS_p:age	1.228	0.462	1	5.860	0.015
$density_p$:age	0.037	0.021	1	1.783	0.182
BCS_c:$density_c$	0.040	0.058	1	0.287	0.592
age: BCS_c	−0.672	0.703	1	0.530	0.467
age: $density_c$	−0.018	0.029	1	0.883	0.347
BCS_p:$density_p$:age	0.040	0.035	1	1.297	0.255
BCS_c:$density_c$:age	−0.046	0.058	1	0.634	0.426

Table 3.5. Analysis of yearly reproductive success for adult (ages 4 years +) female feral horses on Sable Island, Nova Scotia in relation to skeletal size (Height, Length and Heart depth) and body condition score in the summer of conception (BCS_c) and using generalized linear mixed effects models with binomial error distribution and complementary log-log link function (model M_{SIZE}). Data includes 378 observations of 128 horses over 4 years (2009–2012). Horse ID and year were incorporated as random effects. Colons denote interaction terms.

Parameter	**β**	**SE**	***df***	**Wald X^2**	***P*-value**
BCS_c	0.283	0.133	1	4.160	0.041
Heart depth	0.136	0.068	1	3.679	0.055
Length	−0.024	0.027	1	0.800	0.371
Height	−0.078	0.044	1	2.919	0.088
BCS_c:Chest	−0.084	0.101	1	0.687	0.407
BCS_c:Length	0.027	0.044	1	0.386	0.534
BCS_c:Height	0.062	0.071	1	0.774	0.379

Table 3.6. Reproductive output of sub-adult female horses from Sable Island, Nova Scotia (2008–2012), the Granite Range, USA (1979–1983, Berger 1986) and Misaki Range, Japan (1979–1993, Kaseda et al. 1995) based on stability of consort relations with the number of observations in each category (*n*). Sable Island values are yearly reproductive success rates (production of a foal that survives to yearling age) and Granite and Misaki Range values are foaling rates (birth rates). Sable Island and Misaki Range values are for three year olds. Granite Range values are for two and three year old females.

Location	**Category**	**Rate**	***n***
Sable Island	Stable	0.215	79
	Unstable	0.119	126
	Average	0.162	222
Granite Range	Stable	0.57	30
	Unstable	0.08	12
	Average	0.40	23
Misaki Range	Stable	0.429	21
	Unstable	0.118	17
	Average	0.360	26

4.0 CONCLUSION

Berger (2012) felt the use of photogrammetry might be restricted as certain conditions may inhibit its implementation (e.g., forest habitats, time of day), and size-mass relationships must be validated and may be difficult to determine non-invasively for some species. However, photogrammetric studies have been able to measure individuals over long distances (Durban and Parsons 2006; Willisch et al. 2013) or underwater (Deakos 2010), clinometers have allowed use on arboreal monkeys (Rothman et al. 2008) and blinds or vehicles may allow the technique to be used around bait or common feeding, watering, and resting sites for less approachable species (Bergeron 2007).

The parallel-laser photogrammetry technique I described was able to give accurate body size estimates of curvilinear traits in free-ranging mammals. By testing my methodology on domestic Newfoundland ponies, I identified reliable and accurate morphometric variables to use in my study of reproductive ecology, as well as unreliable variables to avoid. I'd recommend that a pilot study be performed prior to the application of this technique on target populations. Parallel-laser photogrammetry could be used for a variety of other terrestrial or aquatic animals, particularly those that may be approached relatively closely, such as Soay sheep, seals and human-habituated wildlife such as townsite elk and deer. Photogrammetry is relatively inexpensive (Berger 2012), which is beneficial for long-term monitoring programs. In addition, photogrammetric photographs can be collected and stored when funding is limited, and measured later when funding becomes available and technicians can be hired. The technique is advantageous for studies of reproductive ecology because it removes the need to capture, handle

or chemically immobilize subjects (Bergeron 2007), which can affect female reproductive output (Côté et al. 1998).

Age is one of the most influential factors in the reproductive ecology of female horses. Age effects are responsible—partially or in full—for trends previously associated with body size (e.g., Duncan 1992) or reproductive experience (e.g., Berger 1986). Differences between the age classes due to energy budgets or social and sexual behaviour caused relationships that were more pronounced in sub-adults (i.e. body condition at parturition) or only evident in adults (i.e., body condition at conception, stability of consort relations). However, age is not the only factor determining reproductive success on Sable Island as somatic fat reserves, local density and stability of consort relations all have their own roles. The year-round social associations of both sexes in horses produce a combination of patterns in their female reproductive ecology similar to those observed in capital breeding ungulates and social primates. In addition, although not detected here, weather influences population dynamics with adverse acute events that are sporadic and can have detrimental effects on the reproductive output in a given year (Welsh 1975).

The reproductive ecology of female horses is much more complicated than what I presented here. The monitoring program of the Sable Island horses is in its infancy; the relatively short duration of data available for this study limited the analyses that could be conducted to short-term effects on yearly reproductive success for broad age classes. In addition, skeletal size data were so limited for sub-adults that I could only analyze size influence in adults. Skeletal size—in combination with fat reserves—potentially has an influence on the reproductive output or age of primiparity of young females (Green and Rothstein 1991). With sufficient data for known age females, the adult age class could be grouped into more informative categories and

the reproductive ecology of prime-age and reproductively senescent females could be analyzed separately. Long-term effects of social experiences or reproductive history may also be performed. This long-term data set is essential to understand population dynamics and reveal the evolutionary forces at work on Sable Island.

When studying reproductive ecology, the choice of reproductive variable (i.e. pregnancy rates, foaling rates, etc.) can greatly influence the conclusions (e.g., studies of Kaimanawa horses, Linklater et al. 1999; Cameron et al. 2003; 2009). For K-selected species, it is important to choose variables that measure reproductive output after the many factors affecting conception, gestation or early offspring mortality have acted. Although differences in pregnancy and foaling rates due to maternal life history may be evident (e.g., Linklater et al. 1999), if they are no longer present after most of the cohort is weaned or reaches sexual maturity, they might not translate into variations in fitness of the mothers. However if cross-generational effects resulting from maternal life history influence the reproductive potential of offspring, even without differences in reproductive output, the fitness of the mother can still be influenced by certain life history factors (e.g., recent reproductive history, Green and Rothstein 1991). This is the next step in the study of reproductive ecology of female horses on Sable Island.

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APPENDIX A: VARIABLE DESCRIPTIONS FOR LIFE HISTORY CHARACTERISTICS OF SABLE ISLAND HORSES

Age class in the year of parturition (age): categorical

Sub-adult - three-years of age

Adult - four-years of age or older

Yearly reproductive success for the year of parturition (YRS): binary

Category 1 - foal born and survived to yearling age

Category 0 - no foal born/foal born but died before 1 year of age

NAO index in the winter following conception/parturition (NAO_c/NAO_p): numerical

The average of NAO index values (difference in normalized sea level pressure between Gibraltar and SW Iceland) over the winter months (from December to March, see Osborn et al. 1999). In the eastern United States, strong positive values are associated with warmer and wetter than average winters, strong negative values are associated with colder than average winters with the potential for large snowstorms.

Local density in the summer of conception/parturition ($density_c$/$density_p$): numerical

The number of individuals per km^2 of vegetated area within an 8000 m buffer surrounding the focal individual's median location.

Parity status in the summer of conception ($parity_c$): categorical. I assigned parity status to mares for years when sufficient knowledge of reproductive history was available.

Nulliparous - mares had given birth to no foals previously

Primiparous - mares had given birth to one foal previously

Multiparous - mares had given birth to two or more foals previously

Band structure in the summer of conception/parturition ($structure_c$/$structure_p$): categorical

Single-stallion - band had one male over four-years old

Multi-stallion - band had two or more males over four-years old

Stability of consort relationships in the year prior to conception ($stability_c$) or from conception until parturition ($stability_p$): categorical

Unstable - mares joined a family band since the last field season

Stable - mares sighted with the same band stallion for at least one year

Age of primiparity ($parity_{age}$): categorical

Sub-adult - females were three-years of age or younger at the time of parturition of their first foal

Adult - females were four-years of age or older at the time of parturition of their first foal